THE FEEDING BEHAVIOUR OF ALPINE GRASSHOPPERS (ACRIDIDAE : ORTHOPTERA), IN THE CRAIGIEBURN RANGE CANTERBURY, NEW ZEALAND

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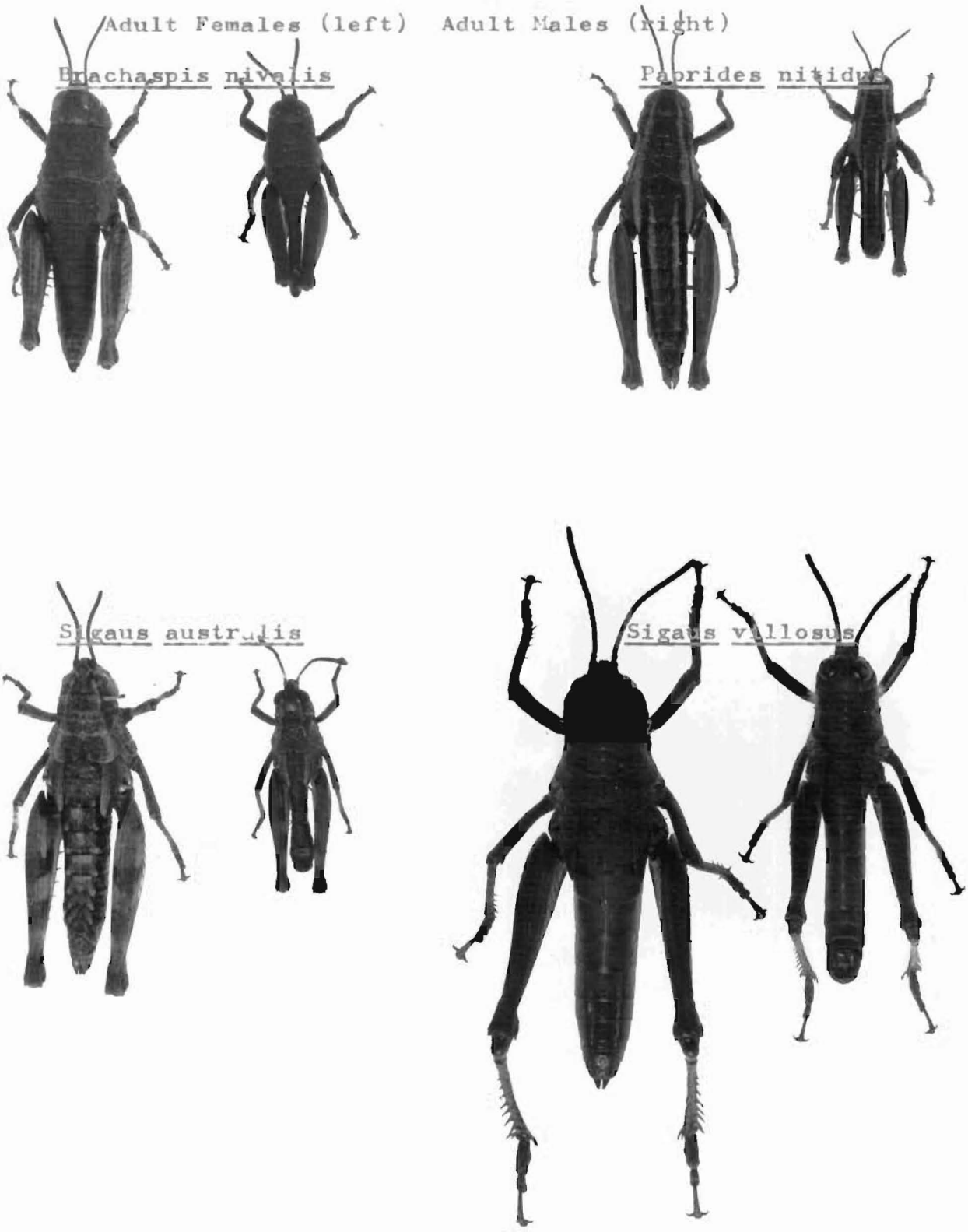

FRONTISPIECE

The Four Species of Grasshopper investigated in the Present Study

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CHAPTER 1

INTRODUCTION

"There is every likelihood that present deterioration evident in (New Zealand) alpine grassland may be caused in large part by insects that feed on leaves, seeds and roots of the plants ....." (Howard, 1966)

The critical importance of vegetation cover to the stability of alpine areas, and ultimate to the amelioration of hydrological characteristics in lower catchment areas, has been given wide emphasis. The present poor condition of much of the alpine vegetation for watershed protection, with extensive development of erosion as a result, has been attributed to many contributing factors. Such factors pertain to:

> the nature of the parent material, and topography; climatic changes and the intensity of frost, wind and rain; and influences since the occupation of humans including the pre- and post-European use of fire, and the effects of grazing animals.

However, the impact that insects might have on the vegetation has, for several reasons, been almost entirely overlooked. Firstly the effects of insects have been overshadowed by the more apparent factors included above. Furthermore the insects involved are endemic, inhabiting what is still essentially an indigenous habitat. In this light, insects are often regarded as "fully adapted" or "in phase" with the environment and therefore of no consequence in influencing change in the vegetation. Although the plant species of alpine regions are indigenous, it is well known that great changes have occurred in the equilibrium and structure of the cover, largely as a result of climatic changes which were greatly aggravated by the man induced stresses of pre- and post-European eras. Just as grassgrub and porina have responded to dramatic changes in the lowland environment, so too it is not unrealistic to assume that the bionomics of alpine insects might in some way have altered from those operating under more pristine conditions.

Lastly, in an economic sense alpine grassland is, at best, exploited on a very extensive scale, having been used as summer grazing for sheep. As a result the associated insects have escaped prominence as direct competitors with man's interests.

The need to define the role of insects in native vegetation has been expressed by Hoy (1964) and Howard (1966). Batcheler (1967) strongly implicated the grasshopper as an agent in alpine grassland deterioration. Hence, as a

preliminary to defining the influence of insects on the pattern processes of alpine vegetation, it was decided to investigate the feeding habits of the most apparent insects concerned, the grasshoppers.

The most important aspect of this study was a determination of the diet of grasshoppers, to ascertain if feeding pressure could be exerted on particular components of the vegetation, as a result of the plant species selected. This involved the determination of diet in relation to the associated vegetation. To this end, grasshopper diet was largely determined from the analysis of gut contents, and vegetation was assessed by the point analysis method. The main bulk of field work was carried out in a study area in the Craigieburn Range, Canterbury, during the summer of 1968/69.

A secondary aim was also facilitated from the diet determinations. An investigation of the degree of food specialization between the four grasshopper species concerned, whose feeding ranges overlap, enabled some indication of the possible extent to which intraspecific competition for food was present.

CHAPTER 2

REVIEW OF LITERATURE

INTRODUCTION

Grasshoppers belong to the insect order ORTHOPTERA. The economic importance of many Orthopteran species, together with a generally large size and favourable laboratory rearing characteristics, has encouraged a considerable, though diffuse literature on many aspects of their study. For convenience this review is divided into sections under the following general headings:-

1 : Economic importance of orthopteran insects in New Zealand.

2 : Taxonomy and distribution

3 : General ecology of Acrididae

4 : Food selection by grasshoppers

5 : The determination of diet in grasshoppers

6 : The alpine grasshopper

1 ECONOMIC IMPORTANCE OF ORTHOPTERAN INSECTS IN NEW ZEALAND

The order Orthoptera includes among its members the shorthorned grasshoppers, locusts, crickets, katydids, long horned grasshoppers and wetas. The order is much more fully and diversely represented in low latitudes where, largely due to the notoriously devasting destruction caused by periodic locust and grasshopper plague outbreaks (Bullen, 1966), it assumes major economic importance in agriculture.

Orthopteran insects are of very minor significance in New Zealand agriculture. Cumber (1959), and Cumber and Eyles (1961) surveyed the insects of pasture and fodder crops in the North Island, and found seven species present representing three families. Of these, only the black field cricket (Teleogryllus commodus Walk.) causes periodic severe but local damage to pasture, principally on the Hauraki Plains and other northern North Island areas. The katydid species (Caedicia simplex (Walk.)) is of slight economic importance to horticulturalists, mainly in citrus orchards (Cottier, 1966).

Of the shorthorned grasshoppers, the only recorded instance where damage levels required remedial action, occurred to lucerne and fodder crops in the Rangitata River area of South Canterbury, by the small lowland species, Phaulacridium marginale (Walk.) (Lowe, 1956).

However, as alpine grasslands presently bear

connotations of potential for watershed protection rather than production in the agricultural sense, the role of insects in such areas should be regarded in the light of unfavourable influences on the cover rather than production. This implies investigation into the long term effects of the population on the floristic composition; vigour and regenerative capacity of the vegetation. In this light Batcheler (1967) suggested strongly that alpine grasshoppers could be of significance in alpine vegetation.

Batcheler (1967) studied the ecology of grasshopper populations of Cupola Basin, in the Nelson Lakes district. The taxonomical work of Bigelow (1967) is the only other publication including information on the distribution behaviour and bionomics of New Zealand grasshopper species.

2 TAXONOMY AND DISTRIBUTION

Shorthorned grasshoppers and locusts are included in the Family Acrididae, the largest family in Orthoptera and containing half of the 20,000 odd known species (Key, 1970). The position of Acrididae in the taxonomic hierarchy is as follows (Imms, 1957) :-

Class	:	Insecta
Order	:	Orthoptera
Suborder	:	Caelifera

Super family : Acridoidea

Family : Acrididae

Acridoidea is given suborder status in the revision by Dirsh (1961), who divides the taxon into 14 families. The family Acrididae is in turn constituted of 19 tentative subfamilies.

Classification of New Zealand Acrididae

The acridid fauna of New Zealand was reviewed by Bigelow (1967). In keeping with other temperate oceanic regions, the fauna is a limited one, being restricted to fifteen species. All of these belong to the family Acrididae. With the exception of the pandemic species Locusta migratoria L., an Oedipodinae, all species are endemic and are considered by Bigelow (1967) to belong to the subfamily Catantopinae. Some ninety percent of Australian acridids also belong to this family, which in marked contrast to the New Zealand fauna, contains 584 species (Keys, 1970).

Affinities. Australia and New Zealand share only one genus, of which the single endemic New Zealand species, Phaulacridium marginale appears to have close relations with Australian species, to the extent that F_1 hybrids have been obtained with P.vittatum. P.marginale is thought possibly to have immigrated to New Zealand in postglacial times. Rare adult individuals of this species occur in macropterous condition, in contrast to the remaining New Zealand species

which are all brachypterous (Bigelow, 1967). These latter species are thought to have been derived from autochthonous ancestors since the geographical isolation of New Zealand. The cold temperature adaptations which now confine all but one of these species to the alpine environment is considered to be a consequence of surviving the Pleistocene glaciations, together with an absence of suitable grassland vegetation in lowland areas when climatic conditions permitted a forest cover (Bigelow, 1967). On the basis of affinities with Tasmanian and Chilean grasshopper forms, Bigelow considered the New Zealand fauna to be of Paleoaustral, rather than of Austromalayan origin. Kay (1970) concluded that the mainland Australian fauna consisted of elements of ancient autochthonous origin, and from the Malay biogeographic region. It is interesting to note that he considers that the most successful Australian alpine species originated from the latter region. The apparent absence of affinity between the alpine grasshoppers in the alpine region of south-eastern Australia and those of New Zealand appears unusual, particularly in view of the wide similarity in the vegetation of the two regions, which have much in common at generic and even specific levels, as evidenced by McVean (1969).

Genera and species. Besides Locusta and Phaulacridium, the remaining 13 New Zealand species occupy four genera; Sigaus, Paprides, Brachaspis and Alpinacris. Of these, the genus Alpinacris and no fewer than six species

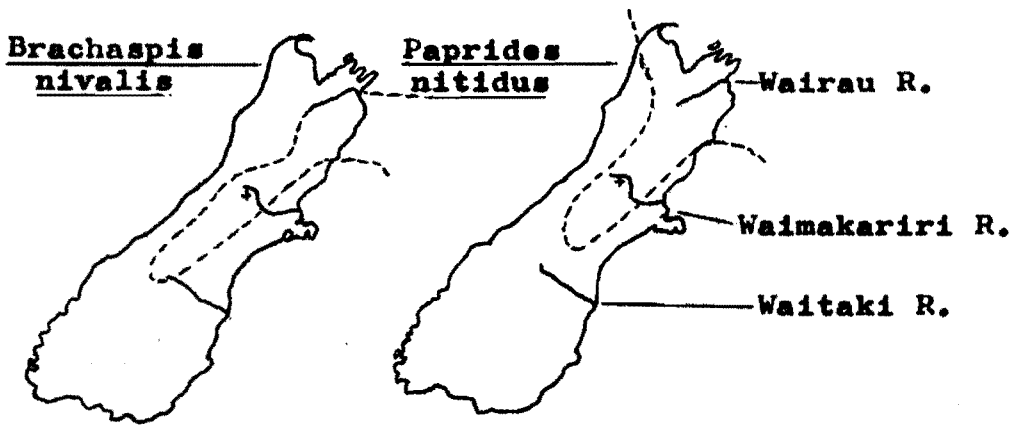
including members from each of the other genera were described by Bigelow (1967).

With the exception of Sigaus campestris Hutton, although including the single North Island species S.piliferus Hutton, all 13 species are eualpine, being confined either above timberline or to grassland vegetation above about 3,000 feet in altitude. The grasshoppers occur in greatest profusion in the drier mountain areas e.g. east of the Main Divide in the South Island.

The grasshopper species may be divided into two groups on the basis of their preferred habitat types and which is reflected in their protective colouration. One group occupy sites on or near screes and shelter beneath rocky scree debris. The basic colouring of these species is grey. The other group occupy tussock grassland vegetation and shelter under dense vegetation. These species are shaded variously in greens and browns.

The present study involved an investigation of the feeding habits of four of these species, representing three genera, comprised of Brachaspis nivalis (Hutton), Sigaus villosus (Salmon), S.australis (Hutton) and Paprides nitidus (Hutton). The first two were of scree habit types and the last two occupied vegetation.

Distribution of species. Bigelow (1967) defined the geographical limits of the New Zealand grasshopper species. The distribution of the four species included in the present



SOUTH ISLAND, N.Z.

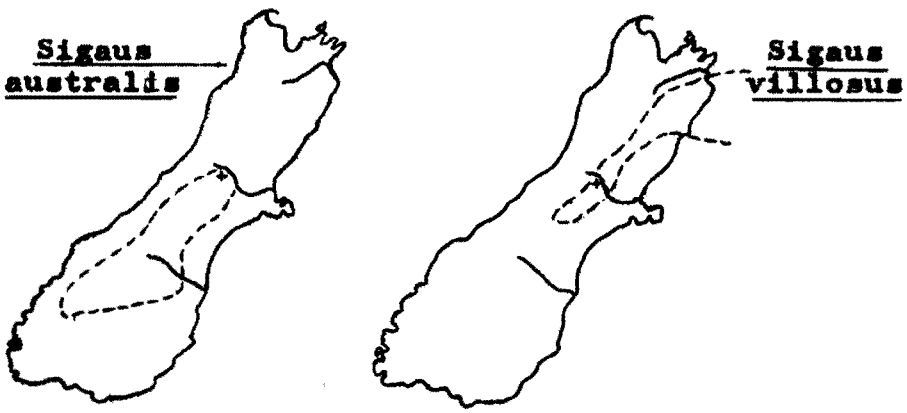


Fig. 1 Distribution of Craigieburn[+] Grasshopper species (after Bigelow, 1967)

study is illustrated in figure 1.

S.australis is common at higher altitudes from the south bank of the Waimakariri River to the Clutha catchment. The species prefers altitudes above 4,000 feet.

The remaining species have a more northerly distribution. B.nivalis occurs above 3,000 feet on rocky ridges, screes and scree verges east of the Main Divide from the Wairau River in the north, to northern areas of the Waitaki Catchment in the south. S.villosus occupies rocky bluffs and ridgetop sites above 5,000 feet in eastern mountain areas between the Wairau and Rangitata River areas. P.nitidus is present in the mountains of North West Nelson, and from the Wairau to Rangitata Rivers, occurring in vegetation above about 3,000 feet.

Intraspecific variation. The present altitudinal limitations of alpine species restricts these grasshoppers to a series of mountain "island" populations. The reproductive isolation of such populations is therefore presently conducive to the development of regional intraspecific variation. However the limited time period for which these conditions have been operating, appear to have confined such regional variation to rather minor morphological differences. (Bigelow, 1967; Peterson, 1969).

3 GENERAL ECOLOGY OF ACRIDIDAE

Introduction

While the general behavioural ecology of Acrididae bear overall similarities (and observations made on species of the present study indicate no exception), it must be borne in mind that many different species and circumstances are discussed in the literature in which peculiarities occur at all taxonomic levels.

The Acrididae are best represented in tropical and continental areas, particularly where a dry climate is conducive to the development of an open terrestrial habitat, characterised by grassland vegetation.

Grasshoppers are generally of diurnal habits. The night, and unfavourable climatic periods, are spent under cover of dense vegetation, while the daylight hours are occupied in basking, feeding and reproductive activities on more open sites.

The insects are saltatorial, and phytophagous, possessing mandibulate, usually hypognathous mouthparts which bear a strong series of grinding ridges (Imms, 1971). Species within the various subfamilies tend to exhibit broad trends in host plant selection. The Catantopinae which includes the New Zealand grasshoppers, were observed by Isley (1944) to be generally of forbivorous (broadleaf feeding) habits rather than graminivorous.

Life cycle. Although variously adapted to local conditions, the life cycle is usually univoltine. It often includes a diapausing stage, usually embrionic, which is regulated either by a dry season or cold temperature. Grasshoppers of warm areas without a marked seasonal influence, may have more than one generation per year. e.g. some Nigerian species (Golding, 1948). The three to four year life cycle exhibited by the New Zealand alpine grasshoppers (Batcheler, 1967) appears to be decidely atypical.

The female grasshopper characteristically lays eggs in the ground, using the short curved valves of the ovipositer to excavate a hole. The mass of up to thirty or more eggs is exuded with a glutinous fluid which hardens to form a protective pod.

After hatch, metamorphosis is slight, with a variable number of four to eight or more instars. A comprehensive treatment of acridid morphology, physiology and development is given by Uvarov (1966).

Factors determining the Distribution of Grasshoppers

In common with all animals, the occurrence and abundance of grasshoppers is determined by factors of the biotic and abiotic environment. In more specific terms these include (Clark, 1948):-

(i) climatic conditions both local and general

(ii) supply of food

(iii) suitable sites for reproductive activity

(iv) interspecific parasite/predator/competitor relations.

Vestal (1913), Isley (1937, 1946), Anderson and Wright (1952), Anderson (1964a), Nearney (1961), Reigert et al (1965) and Riegert (1968) are among those who included some general observations on the habitat preferences and requirements shown by North American grasshopper species; while Clark (1948), Dreux (1961), Kaufman (1965b), Kopaneva (1963), Clerk (1947 a, b) and Anderson (1964b) have done so in varying degrees of specificity for British, French, Bavarian, Caucasian, Australian and East African species respectively. Most of these authors gave emphasis to the importance of climatic conditions of the Acridid environment in determining the distribution of grasshopper species. In more general terms Kopaneva (1963) and Kaufman (1965b) discuss the effects of moisture on grasshopper distribution. Kaufman (1965b) grouped species as xerophilic, hygrophilic or mesophilic, according to their occurrence in dry, moist or intermediate areas. As a group however, Acridids tend to prefer drier habitats and low humidity.

Most observations by the above authors on the preferred habitat of grasshoppers, are confined to a more local level. In particular the microclimatic temperature and humidity, as influenced by topography, and nature of the vegetation, was considered to determine the distribution of grasshoppers.

The structure (height and density), and taxonomic composition of the vegetation were regarded as the principal components influencing grasshopper bionomics within a habitat.

Influence of species composition of vegetation. Opinions differ as to the role of the floristic composition of vegetation in the distribution and abundance of grasshoppers. The plant species may be indicative of the local conditions of climate, moisture etc., which may also be defining the geographic range of the grasshopper. Furthermore, since grasshoppers are dependent on the vegetation not only as food, but also for shelter, the distribution of favoured food plants may not necessarily coincide with that of a grasshopper species. For instance, Kaufman (1965a) found that Zonocerus variegatus L. was restricted to plant associations which satisfied its roosting behaviour.

While grasshopper species vary in their feeding habits from unselective to highly selective feeders (Anderson 1964a), the majority, without being rigid or inclusive, exhibit well marked preferences. Where feeding habits are general rather than specific the food selected by grasshoppers under natural conditions is greatly dependent on the abundance of plant species in the habitat (Mulkern, 1967). Pruess (1969) found that while Phoetaliotes nebrascensis (Thomas) generally occurred in greatest numbers in association with preferred host plants, populations were also supported in otherwise suitable habitats. Anderson (1964a), in finding that grasshoppers did not occur in

the absence of favoured food species, concluded that the taxonomic composition was an important factor, although changes in grasshopper abundance did not relate to the abundance of primary food plants in the habitat.

The importance given to the floristic composition by many North American authors (Isley, 1938a, 1946; Anderson and Wright, 1952; Anderson, 1964a) compared to British authors (Clark, 1948; Williams, 1954), could possibly be attributed to the greater diversity in the American rangeland fauna, resulting in a greater degree of specialization in feeding habits.

The distribution of grasshoppers, even within a seemingly uniform area of occupation, is highly non-random (Anderson, 1961). Although social behaviour may be partly responsible, this phenomenon has largely been attributed to klinotactic responses of grasshoppers to unfavourable situations (Clark, 1948; Chapman, 1957; Anderson, 1961). Grasshoppers move more frequently and further in such situations, resulting in local aggregations on the site of favourable microclim atic conditions or food plants. In this way plant species do have an influence on the local distribution within a general habitat.

Influence of vegetation structure. The height and density of the vegetation cover appear to bear the greatest influence on local grasshopper distribution. Clark (1947a, b) recognised two habitat types required by Chortoicetes terminifera Walk. and Austroicetes cruciata (Sauss):-

(i) a food/shelter habitat, preferably sites containing some tall tussocky vegetation, with low cover in excess of the tall vegetation.

(ii) an oviposition habitat, the requirements for which were bare soil and low vegetation cover.

This optimal food-shelter habitat type best suited the diurnal habits of grasshoppers, as well as favouring the growth of the more succulent, minor plant species preferred as food by grasshoppers. The quality of oviposition sites was also found to be influenced by conditions of soil moisture, compaction and temperature (Clark, 1947a, Reigert et al, 1965). Largest populations were observed to develop where these habitat types overlapped. Reigert et al (1965) found that such conditions were provided for Camnula pellucida (Scudder) where the short Canadian rangeland native grassland (oviposition site) bordered cereal crops (a favoured food habitat).

In most natural situations these dual habitat requirements exist in a mosaic pattern within a general area of occupation. In these areas, highest numbers were found by Smith (1940) to be developed within sparse vegetation before the appearance of severe erosion. Anderson (1964a) found that the optimal areas of occupancy were provided where the percentage foliage cover was below 40% in plains areas, and about 60% in mountain habitats.

Although the nature of vegetation cover is important by virtue of its influence on the microclimatic environment, little

has been done to investigate the relationships between the vegetation and microclimate as it affects grasshopper distribution and daily behaviour patterns. Grasshoppers exhibit and actively seek an optimum range of temperature and humidity conditions which Mulkern (1967) found in reviewing literature, to lie generally between 70° and 90°F at less than 50% humidity. Uvarov (1948) reviewed work, mainly Russian, which showed that the internal temperature of grasshoppers, while dependent on that of the surrounding air, is also influenced by physiological processes and other factors of the grasshopper, e.g. colour, and external factors influenced by the vegetation structure, e.g. effects of shade and wind. While the internal temperature of grasshoppers was up to 10-15°C higher than ambient in sunny situations, shade negated this differential. Grasshoppers were considered to relinquish the open sites when the temperature differential between the two coincided. The reverse took place in the morning as the temperature of open sites rose above those at the base of dense vegetation.

Topography. The topography bears an important influence both on the macro- and microclimatic environment. Topographical features are particularly important in the alpine environment, especially in respect of altitude, slope and exposure to wind and sun. For instance grasshoppers in New Zealand are largely confined to altitudes above 3,000 feet, below which the temperature is probably not

sufficiently rigorous to satisfy a cold temperature requirement in the life cycle, probably an embryonic diapause (Bigelow, 1967).

A greater degree of exposure to sun has the effect of decreasing the density of vegetation especially when associated with dryness of soil, wind and grazing (Clark, 1948). Such sites are therefore more favourable to the thermophilous grasshoppers, which by comparison, are present in very low numbers in cold shady situations.

Factors Influencing the Abundance of Grasshoppers

Effect of changes in the vegetation. As the nature of vegetation is of such importance in grasshopper ecology, the factors which influence its composition are of interest, particularly in respect of changes incurred by the cultural and agricultural practices of man. These have often had a profound and favourable influence on many grasshopper habitats, more usually in open rangeland situations. In general those factors which lead to a more open habitat, while maintaining some rank cover for shelter, favoured an increase in grasshopper numbers.

Climax grassland vegetation is in general characterised by a low bulk of broadleaved species which are able to increase as the cover becomes more open (de Vos, 1969). The influence of grazing animals on the structure and composition of vegetation, and subsequently the grasshopper abundance is

particularly marked. Reigert (1968) indicated the importance of buffalo in maintaining a favourable open cover for grasshopper under pristine North American range conditions.

Overgrazing, especially by sheep in dry rangeland conditions have been attributed to increases of grasshopper populations following the opening of cover and onset of erosion in Australia (Clark, 1947b; Andrewartha, 1945) and in North America (Dibble, 1940; Smith, 1940). Smith (1940) found that on overgrazed Oklahoma range country, a greater number of grasshopper species, and four times the total population levels were present compared with normal grassland. He found that populations declined however, on severely eroded land as the food/shelter habitat became deficient. Closely grazed swards produced by grazing in moist and temperate lowland situations do not favour grasshoppers, and they become restricted to the more rank roadside, and other waste areas. (Clark, 1948).

The use of fire has also been an important influence in vegetation, being responsible for both extending and maintaining large areas of the world's grassland climatically suited to forest growth (de Vos, 1969), as well as influencing the nature of grasslands as reviewed by Daubenmuire (1968). The overall effects of repeated burning were seen to be a weakening of the dominant species and an opening of cover, especially when combined with grazing. There was a subsequent succession by fire resistant species of plants which tended

to be of lower growing forb species. Because of their growth habit and greater succulence, these species tend to produce less voluminous and less flammable litter than do the original grasses.

Tester and Marshall (1961) indicated that grasshoppers showed preference for the succulent vegetation produced during recovery from burning. There is an absence of information on the short and long term effects of burning of vegetation on grasshopper populations.

Changes in grasshopper numbers induced as a result of agricultural cultivation practices do not seem to have been as profound, although Reigert et al (1965) noted that cereal cultivation in North America provided Camnula pellucida with a superior food source to that of the natural grassland environment. This insect became a particular pest where wheat bordered areas of native grassland in which it could breed. More severe grasshopper infestations were observed by Dibble (1943) and Andrewartha (1943) to develop on lighter soils and abandoned agricultural land than in more fertile areas. Poor conditions of soil moisture, fertility and texture tend to reduce the height and density of dominant species and associated plant species become more abundant. The slower recovery from stress periods under these unfavourable situations also tends to prolong and maintain irregularity in the vegetation.

Population regulating mechanisms. The major plague

outbreaks of grasshoppers and locusts are generally confined to hot, arid areas. Climatic factors appear to play the most influential role in regulating population outbreaks. The highly fluctuating mortalities which are primarily responsible for regulating the dynamics of populations (Pottinger, 1967), appear to occur mainly in the egg stage. Birch and Andrewartha (1944), Clark (1947b), Hogan (1965), Pickford (1966), Reigert (1967b), Storer and Greathead (1969) indicated high mortalities to eggs resulting variously from causes of drought, heat, frost or excessive moisture.

High grasshopper population densities may also arise from the direct or indirect effects of a favourable growing season on the condition of the vegetation. Where such a response occurred, low numbers again followed in dry seasons (Popov, 1963; Nearney, 1961; Nearney and Hamilton, 1969). In these circumstances, limitations of food and shelter operated on post-embryonic stages, to regulate the population as indicated by Nearney (1961).

Very dense populations do not appear to occur in grasshopper populations of temperate, moist regions. Clark (1948) attributed the generally low populations in such areas to a lack of oviposition sites. This reason, if correct, combined with the fact that the predominantly perennial vegetation is very much more uniform in seasonal productivity and condition than the annual type of counterpart in hot arid areas, possibly contributes to the relative constancy of grasshopper numbers.

The role of other population regulating factors such as predators, parasites and disease is an undefined one. This is very largely because of a lack of investigation into the population dynamics of grasshopper populations of the type permitting analysis of mortality. Populations are usually determined statically, to relate these to damage inflicted on the vegetation, and to determine the need for control measures, e.g. Anderson and Wright (1952) and Nearney (1960). Egg surveys are also performed as an aid to forecasting population outbreaks e.g. Reigert (1968).

Although symptomatic of the dearth in work of this nature, the fact that mortalities caused by biotic factors seldom receive comment suggests that these are of very minor significance in the regulation of natural populations. Ball (1937), without data, stated that parasites, predators and disease were responsible for the decline in grasshopper populations following build up after a favourable climatic period in some southern North American States.

However, the night-time inactivity of grasshoppers would indicate a vulnerability to nocturnal predation. Furthermore, the very high degree of cryptic colouration developed in grasshopper species indicates that selective pressure for camouflage is, or at some time was, probably intense. In this latter respect Isley (1938b) was able to demonstrate the value of protective colouration in bird predation by mounting grasshoppers on and away from their natural backgrounds.

Destruction by Grasshoppers

Nature of damage inflicted. The damage inflicted by grasshoppers is principally one of defoliation. Grasshoppers feed largely on the margins of the leaf lamina, in a manner described by Williams (1954) and Gangwere (1960, 1965a). Grasshoppers also consume flowers, buds, stems, green bark and seedlings, with possibly a greater significance to the conditions of the vegetation than the feeding on mature leaves. As pointed out by Kelly and Middlekauff (1961), damage also extends beyond that actually consumed. Wastage from feeding occurs with the severence of leaves at variable distances along the margin. Plants may also be damaged or killed by excessive defoliation or bud nipping, growth is retarded, and rejuvenation from reseeding is impaired, resulting in exposure of soil to erosive forces.

Estimation of damage. Evaluation of damage caused by grasshoppers is achieved by a number of methods based on the following:-

(i) Laboratory studies

(ii) Field estimations

(iii) Energetical studies

Laboratory studies generally involve the effects of temperature and humidity on development, activity and food consumption. The food consumption is estimated from leaf area or weight consumed. As to be expected, the quantity of food ingested increases with the body weight and activity of grasshopper

individuals, but is also related to species. Gangwere (1959) found that although adult females of Melanoplus s.scudderi (Uhler) were about twice the weight of males, the feeding disparity was less than double, which was attributed to their lower general activity. This state is a typical occurrence in grasshoppers. Further to this, Davey (1954) and Kaufman (1965b) found that male grasshoppers assimilated a greater proportion of ingested food than did females. Williams (1954) observed that males had a longer feeding time than did female grasshoppers, which in turn probably fed more frequently. Bullen (1966) stated that in general terms nymphs ate roughly their own weight of fresh vegetation per day, while adults consumed half this ratio.

Estimations of damage by field estimation have been made by the use of exclusion techniques with cages (Putman, 1962) or from areas sprayed and unsprayed with insecticide (Anderson and Wright, 1952; Anderson, 1961). Nearney (1960) estimated the total damage to vegetation from that inflicted on individual plants which were assessed in the field. Such a method neglects to take into consideration the indirect losses in production resulting from feeding. Field damage by grasshoppers is usually expressed on the basis of the numbers per unit area.

Because of the very non-random distribution pattern of grasshopper populations, Anderson (1961) considered it was fallacious to calculate damage over a large area based on the findings in a small area. This situation is further

complicated by the feeding preferences of grasshoppers. Anderson and Wright (1952) concluded that damage to vegetation needed to be evaluated on the basis of the species of grasshopper present, as well as the composition and condition of the vegetation, and could not be accurately determined solely on abundance of grasshoppers.

Bullen (1966) considered that the mobility of locusts played a large part in their standing as a pest. Although the movement of brachypterous grasshoppers is insignificant compared to that of fully winged species (Alexander, 1951), mobility of these species nevertheless plays some role in their damage potential. The mobility of grasshoppers in undisturbed conditions is usually characterised by little or no jumping (Clark, 1948). In dispersal trials using grasshoppers labelled with radioactive bran, Anderson (1961) recovered most within 20 feet of the bait source. Reigert et al (1954) found that seven days after release in a barren area, no fifth instar or adults of Melanoplus species were found greater than 300 yards from the point of release. Only 10% had travelled greater than 100 yards. Within these limits however, the mobility enables an appreciable expression of the innate food preferences of grasshopper species.

The use of energetics (Smalley, 1960; Teal, 1962; Wiegert; 1965) offers the most comprehensive and sophisticated approach to determining the role of insects in the vegetation. As yet the technique is experimentally in its infancy, and

suffers from the disadvantage that it is necessary to extrapolate physiological data determined for individuals under laboratory conditions, to populations in the field.

Intensity of damage. Bullen (1966) considered the intensity of damage was determined by functions according to the expression:

intensity of damage $\int$(amount consumed by individuals,
food preferences,
mobility,
size of population).

The function should include an expression for damage inflicted beyond actual consumption. Bullen (1966) considered that adults were the major source of destruction of vegetation by grasshoppers. Putnam (1962) found that for grasshoppers with an annual life cycle, young adults destroyed as much in five days as in the whole period of nymphal growth. He estimated that, as a general rule of thumb, such a population of rangeland grasshoppers at 10 per square yard, could account for 100 lb per acre of live vegetation from hatch to death.

It is somewhat meaningless merely to quote the absolute damage and populations recorded by numerous authors because of the number of very different circumstances influencing the total damage and the implications of a given level of total foliage removal on any particular site. The significance of an insect population on any location is also dependent on the production and condition of the vegetation, and its value in economic or

conservation terms. However, removal of some 50% of the total vegetative cover appears to be the accepted maximum under good rangeland practices in North America (Putnam, 1962; Bullen, 1966). This figure was frequently exceeded by grasshoppers alone on arid range country. Nearney (1960) showed that an average population of 9 - 27 per square yard caused about 23 - 30% damage on Arizona sites, while infestation of 42 - 64 per square yard caused total destruction of the vegetation produced. On less arid, and more productive situations the destruction is generally much less. Wiegert (1965) found that populations on Michigan oldfield and lucerne respectively consumed 0.5 and 2.5 percent of the net primary production of vegetation.

There is no indication that the accepted 50% level of forage removal is applicable in such situations as the New Zealand alpine areas where recovery from damage is more prolonged, and where weaknesses in the cover are more readily subject to further deterioration. Batcheler (1967), having to use borrowed data to calculate vegetation production and energy requirements of grasshoppers, considered that populations in more open situations in Cupola Basin, Nelson, could probably be consuming anything up to 60% of the total leaf matter produced. The fact that highest numbers are generally favoured on open situations which are more susceptable to erosion, is suggestive that grasshoppers could be a real factor in the aggravation of deterioration of cover, or prevention of

its regeneration in New Zealand.

4 FOOD SELECTION BY GRASSHOPPERS

Introduction

That grasshopper species exhibit varying degrees of feeding selectivity has been widely demonstrated (Mulkern, 1967). The criteria upon which grasshoppers select food is important in interpreting the composition of the diet. General reviews on food selection in insects include those by Fraenkal (1959, 1969), Thorsteinson (1960), and Kennedy (1965), while Painter (1951, 1958) and Beck (1965) discuss this aspect of plant/insect relationships from the view point of plant resistance. More specifically Dadd (1963), Mulkern (1967, 1969) and Gangwere (1961) reviewed literature concerning food selection in Acrididae. Feeding behaviour involves the location and orientation to a suitable food source, and responses subsequent to testing the food resulting in its consumption or rejection by the insect.

Location of Potential Food

Kennedy (1965) divided the mechanisms of host location into those movements which were truly directed and oriented (taxes) and those which were not so obviously directional. These latter movements nevertheless resulted in location of the host either by stimuli from the host arresting the insect

(orthokinesis) or from the random movements of the insect (klinokinesis). It appears that movements of the latter kinds are largely responsible for food host location in grasshoppers. Random movements initiated by a sense of hunger under favourable conditions of temperature, humidity and illumination are responsible for bringing grasshoppers into contact with potential food, or within a range whence somewhat limited olfactory or optical senses may take part (Mulkern, 1967). Chemical stimuli, after contacting a plant, usually form the final criterion by which it is accepted or rejected for ingestion.

Environmental influences affecting feeding activity. Maximum feeding activities observed in laboratory (Chapman, 1965; Dyck, 1969) and field situations (Clark, 1947a; Clark, 1948; Kaufman, 1965a; Ellis and Ashall, 1957) indicated that the optimal ranges generally occurred between 70° and 90°F and less than 50% relative humidity (Mulkern, 1967). Mulkern et al (1962) found that a large proportion of grasshopper crops were empty when specimens were collected following cool conditions in which the grasshopper showed sluggish activity.

Grasshoppers are of diurnal habit, general activity including feeding taking place during daylight hours. Williams (1954) found that feeding in the laboratory was reduced in the absence of light although Kaufman (1965a) found that Euthystira Brachyptera (Ocskay) consumed equal amounts during day and night feeding trials when the temperature was optimal for

feeding. Feeding activity was observed to take place throughout the day, but showed definite peaks, at various times of day for various species by Clark (1947a), Ellis and Ashall (1957) and Abushama (1968a). Chapman (1954) stated that the diurnal activity was a light reaction and not a diurnal rhythm in Locusta m. migratorides, although Abushama (1968a) found that in Poecilocarus hieroglyphicus (Klug), diurnal activity persisted in blinded individuals and those in constant light or dark. He concluded that its operation was endogenously controlled, though synchronised by alternating light and dark.

Perception of light. Positive phototactic responses have been elicited by direct illumination, colour, and visual patterns. Pielou (1948) demonstrated that grasshoppers reacted by positive tactic responses to direct light. Mulkern (1969) showed that this response was independent of heat from the light source in species of Melanoplus. Maximum responses to light were found to occur in the yellow-blue-green wavelength range, with only weak responses from red (Mulkern, 1969). However little response to light attraction in the field has been noted (Mulkern, 1967) this fact possibly being the result of grasshopper inactivity at night.

Visual perception. Caged grasshoppers are frequently observed to show a tendency to crawl up cage walls and objects within the cage (Williams, 1954; Abushama, 1968b). Chapman (1955) showed that such negative geotaxis was overcome when

individuals readily dropped to the floor in response to cold temperature, illumination from below and disturbance. Williams (1954) found that individuals of Gomphocerippus rufus Rob. and Chorthippus albomarginata (Deg.) preferred to rest on a cagewall background of black vertical stripes rather than plain surfaces. Mulkern (1969) also noted that species of Melanoplus crawled up such lines and that this movement was interrupted by horizontal lines. Gardefors (1968) showed that such a preference for vertical stripes was present only in temperature and humidity extremes, and that a plain white background was preferred in intermediate conditions. This corresponded with conditions in which grasshoppers would relinquish dense vegetation for more open sites. Obviously this phenomenon in grasshoppers is a response to an apparent resemblance of vertical lines to the slender vertical grass leaves of shelter positions.

Williams (1954) and Kaufman (1965a) showed the ability of grasshoppers to appreciate form. Kaufman (1965a) found that Zonocerus variegatus could distinguish leaf forms, but did not show a discrimination between host plant and non-food objects.

Wallace (1959), when observing the scanning behaviour in Schistocerca gregaria Forsk. concluded that they could determine distance. Kennedy (1939) and Clark (1947a) considered that visual attraction to conspicuous vegetation occurred up to five yards distance, while Kaufman (1965a) demonstrated an

attraction to vertical objects in Z.variegatus only up to seven centimeters.

Olfaction. Olfactory powers do not appear to be strongly developed in grasshoppers (Dadd, 1963), their role in food location being considered variously as unimportant by Williams (1954), Kaufman (1965a) and Chapman (1955), of some importance by Slifer (1958), to being considered the principal means of food detection in the specialist feeder Poecilocerus hieroglyphicus (Abushama, 1968a). Abushama (1967) showed that olfactory attraction was somewhat increased with starvation. Kennedy and Moorehouse (1969) in studying the effects of windborn grass odour on locust behaviour thought that the positive attraction exhibited was an anemotaxis, although repellence by CCI_4 odour demonstrated olfactory powers. A positive anemotaxis was also noted by Clark (1947a) in Chortoicetes terminifera, while Riegert et al (1965) found that the anemotaxis was reversed in early instars of Camnula pellucida and Melanoplus species. When released in a barren field these grasshoppers showed no ability to orient to distant vegetation.

Discrimination between Food Sources

Chemoreceptors. The appraisal of leaves by application of antennae and mouthpart palpi to the surface of contacted objects, and the indiscriminant biting of plant and non-food items by grasshoppers is a common observation (Clark 1947a;

Williams, 1954; Kaufman, 1965b; Pruess, 1959, and others.) This suggests that the real basis of food selection results from such testing of food after contact is made with it. Biting becomes more prevalent with increasing hunger and water stress, and feeding less discriminate (Mulkern, 1969), although grasshoppers will starve to death in the presence of some unfavourable species (Kaufman, 1965b).

An understanding of the mechanism of food selection requires a knowledge of the receptors involved. Schoonhoven (1968) reviewed plant selection from a chemosensory basis. Dethier (1963) described the ultrastructure of insect sensillae, and their possible functioning from an electrophysiological viewpoint. These sensillae are much modified hairs distributed variously over the insect body surface and function in chemo- and mechano-reception.

Slifer *et al* (1959) showed that such structures located on the antennae of *Melanoplus d.differentialis* (Thomas), *M.m.mexicanus* (Sauss) and *Romalea micropterg* (Beauvois) were probably the chief olfactory organs. Thomas (1966) found a tightly packed group of sensillae on the tip of each labial and maxillary palpi of *Schistocerca gregaria* and suggested that they had a special chemosensory function. Sensillae were found to be similarly distributed in the species *Locusta m. migratoria* (F. and R.) (Le Berre *et al*, 1967; Sinoir *et al*, 1968) and *Poecilocerus hieroglyphicus* (Abushama, 1968a). Haskel and Mordue (1969) investigated the receptors on the antennae and

palps, and also groups of sensillae present on the posterior surface of the clypeolabrum and dorsal surface of the hypopharynx. They confirmed the suggestion of Thomas (1966) that the mouth part receptors on the domes of the palps played an important role in detecting phagiostimulants, and hence in stimulating feeding, while the continued feeding relied on the satisfactory stimulation of the receptors within the buccal cavity.

Role of plant chemicals. Much of the discussion on the theoretical aspects of host plant selection by insects appears to be concerned with which chemical constituents of plants that define feeding. The respective role of plant secondary (non nutrional) substances and common nutrients in determining the acceptance or rejection of food is the main contentious point. Fraenkel (1969) believed that while nutrient substances may have phagiostimulatory action, it is the secondary plant chemicals which determined the acceptance of a plant. Nutrients were precluded in this role both on quantitative and qualitative grounds. The extreme variability in the titre of nutrient substances within any plant species, with different conditions of growth and seasonal and even daily factors, ruled out the possibility of their functioning on a quantitative basis; while these substances are common constituents of all cells, and therefore could not provide a basis for selection on qualitative grounds.

However, many nutrient substances, as well as synthetic

compounds, especially sugars and phospholipids have been shown to stimulate feeding on neutral artificial media (Mulkern, 1967 and Dadd, 1963). The artificial media most usually used is cellulose in powdered, fibrous or filter paper form. Cellulose passes through the grasshopper gut unchanged, enabling the metabolism of impregnated substances to be investigated (Sinoir, 1968). Mulkern (1967) found that grasshoppers exhibited marked selectivity to plant extracts impinged on such media, and that water extracts were preferred over those of ether, acetone and ethanol. By using a nutrient media, with less consequent upset to the metabolism of grasshoppers and thence feeding behaviour, it was also shown the selectivity among plant water extracts persisted in the presence of known nutrient phagiostimulants. It was concluded that feeding occurred in the absence of deterrent substances and in the presence of suitable phagiostimulants, a view expressed by Thorsteinson (1960). More specialized feeders probably make greater use of secondary substances as recognition stimuli, as apparently does the oligophagus Poecilocerus hieroglyphicus to the latex of its favoured host plant, Calotropis procera (Abushama, 1968a).

Fraenkel (1969) had to qualify his former controversial statement (Fraenkel, 1953) to the effect that all plants could potentially serve equally as food on the reasoning that all contained the basic common essentials for support of life. It has been widely demonstrated in grasshoppers and other

phytophagous insects, that wide variations occur in the nutrient balance and efficiency of utilization of different plant species for food. This greatly affects the rate of consumption and the performance of grasshoppers as shown by Barnes (1955), Pickford (1958), Smith (1959), Dadd (1960), Hewitt (1968), Kreasky (1962), Mulkern et al (1962), Mulkern and Toczek (1970). Plant species were shown to vary markedly in the precise effects on growth, size, fecundity, male sterility, and moulting survival of various instars. In general the more preferred species offered their associated grasshopper species the best survival (Chapman, 1957; Kaufman, 1965a, b; Reigert et al, 1965), and mixed diets enabled better performance than single species fed alone.

Mulkern and Toczek (1970) reared Melanoplus fermurrubrum on plant extracts that were incorporated into artificial diets and found that marked differences occurred in survival and rate of development. This demonstrated that the poor performance on certain plants were not entirely due to differences in utilization. They concluded that this effect could be caused by the presence of growth inhibitors, though more probably the lack of a growth promoting factor.

The nutritional requirements of polyphagous species would easily be provided by the combination of food plants consumed in any natural environment (Mulkern, 1967). Many plant species outside the natural range of grasshopper species are nutritionally very adequate, and indeed are often highly

favoured, implying that factors other than diet limit the distributions of most species.

The net effect on food selection, based on a random contact, thence stay-or-leave basis, indicates that the inherent selectivity of grasshoppers would be greatly modified under natural conditions by the availability of plant species, but that a "statistical selectivity" could result from the greater frequency of ingestion of more favoured species when contacted.

5 DETERMINATION OF GRASSHOPPER DIET

Introduction

It was established in section 3 that a determination of the dietary habits of grasshopper species was a necessary requirement for assessment of damage in their associated habitats, and consequently for the assessment of their pest status. Gangwere (1961) and Mulkern (1967) reviewed the methods by which information on the food habits of grasshoppers may be obtained. These normally involved adaptations of the following four principal techniques:-

(i) examination of morphological adaptations to feeding habit

(ii) direct observation of feeding in the field

(iii) differential, or choice, feeding experiments

(iv) analysis of gut contents.

The more comprehensive studies of grasshopper feeding behaviour generally utilized several of these methods, which complement each other.

Morphological Adaptations

Several structures associated with grasshoppers have been noted to broadly reflect the general feeding habits of grasshoppers e.g. mouth part structures (Isley, 1944; Gangwere, 1965), tarsal arolia (Kaufman, 1965b) and morphology of feculae (Gangwere, 1962). The morphological examination of these structures offers no more than a general classification as to feeding type, but do enable a preliminary insight into the expected feeding preferences prior to more extensive investigations.

The most sensitive and therefore most significant of these features as an indicator of food habits, is provided by the dental configuration of the mandibular biting surfaces. Two distinct basic types may be recognised in grasshoppers. Those that characterise a grassfeeding habit contain chizel-like incisors, with a series of ridges and furrows on the molar area, whereas the forbivorous (dicotyledonous feeding)species possess a number of pointed incisor teeth, and molar lobes consisting of several teeth surrounding a cavity (Williams,

1954). An intergradation of these types are indicative of varying degrees of mixed feeding. Kaufman (1965b) also recognised a further distinctive type in moss feeding grasshoppers. Alexander and Hilliard (1964) found that, especially in older adults, wear of the dental surfaces may be considerable, to the extent that the formations may be obliterated.

Isley (1944) classified the feeding patterns of Texan Acrididae on the basis of dental configuration. In general his classification of species showed good agreement with those of other workers, based on field observations and gut analysis (in Mulkern et al, 1962).

Gangwere (1965) extended the observation of morphological features to all of the mouthpart structures, and related their morphology with the general feeding patterns of all Orthopteran types in Michigan. It was also shown by Gangwere (1965a) that as well as relating to the food selected, the mouthpart types also reflected their mechanical use in the taking of food.

Direct Observation of Feeding in the Field

The scattered observations of food selected by grasshoppers, including those species rejected as well as those accepted, appear by many authors (Mulkern, 1967). A few investigators have made more comprehensive observations of the feeding of grasshopper species on botanical associations upon

which they occur. Such investigations are pursued by the painstaking following of the activity of a single or several grasshoppers, and recording plants ingested, merely nibbled and rejected. Anderson and Wright (1952) carried out an intensive investigation of the feeding habits of grasshoppers on Montana rangeland, while Clark (1948), Williams (1954), Gangwere (1960b), Anderson (1964b) and Kaufman (1965a) performed less ambitious observations of this nature on respective local populations.

The advantages inherent in this method are that, where carefully executed, grasshoppers may be observed undisturbed under natural conditions. Much information incidental to food selection may also be acquired on for example social habits, mobility, reproductive behaviour, diurnal behaviour and feeding frequency.

However a major disadvantage in relying on this technique is associated with the difficulty of obtaining sufficiently comprehensive data to enable quantitative and statistically derived functions and conclusions on feeding habits. The tediousness of obtaining data is caused by the extreme wariness of grasshoppers, and periodicity of feeding, which occupies only a few minutes of the total daily activity. Feeding is also greatly dependent on climatic conditions (Mulkern et al, 1962). Consequently most such recordings are of a qualitative nature only, although Gangwere (1961) attempted to relate the incidence of feeding to the relative

abundance of plants as an indication of preference. Clark (1948) to some extent overcame the problems of field observation by confining grasshoppers under jam jars. He assessed preferences by direct observation, and by the relative damage to plants. However the essential feature of the field technique, that of non-interference with natural behaviour, was destroyed.

Differential Feeding Experiments

This technique, essentially a laboratory modification of that described for Clark (1948) above, enables the determination of food preferences in the absence of differences in plant abundance. It usually involves the confining of a certain number of grasshoppers of the same age, sex and species together with two or more plant species, in a cage. The relative acceptability of plant species is either assessed from the number of grasshoppers associated with each plant specimen over a given time period (Williams, 1954), or by estimation of consumption from leaf area or weight loss (Clark, 1948; Kaufman, 1965a,b; Caplan, 1966; Pruess, 1969). Kaufman (1965b) used a ranking system to define relative preferences based on the relative consumption of plants after three days confinement of twenty grasshoppers given a choice of three food sources. The plants were rated on a one to five favourability ranking according to whether the specimens were $>\frac{1}{2}$, $\frac{1}{4} - \frac{1}{2}$, or $<\frac{1}{4}$ consumed, merely nibbled, or untouched.

Although grasshoppers would starve in the presence of some plants (Kaufman, 1965b), selectivity generally decreases with increasing hunger, and grasshoppers progress from more to less favourable foods as they run out (Clark, 1948; Mulkern, 1969). The offering of various combinations of plants in repeated experiments enables the relative preference ranking of all species, associated naturally or unassociated with grasshopper species, to be assembled.

This technique therefore enables some qualitative and quantitative information on the inherent attractions by grasshoppers for plant species, since the abundance factor is eliminated. However because of this, the results bear little relation to the selection of food as expressed in the field, and where the relative abundance of plants in the vegetation is an important determinant (Mulkern, 1967). The method is consequently of little real value when emphasis is on the role of grasshoppers in the vegetation rather than the reverse situation.

The method has further disadvantages associated with the unknown influence of the unnatural circumstances of laboratory conditions on both feeders and food. Caged grasshoppers may behave abnormally due to crowding, or show thermo- or phototactic aggregations, requiring the repeated randomization and shifting of food sources in the cage. Further, the degree of selectivity is influenced by hunger, water-stress, condition of food material, physiological state of individuals, and instar

stage (Gangwere, 1961; Mulkern, 1967). The choice between plant species may be influenced by a varying degree of alteration occurring as a result of cutting or potting treatments, seasonal changes in growth and maturity, or of presentation to the grasshoppers. Because of the subjective assessment of food consumption, and the variability of experimental methods and conditions employed by individual workers using differential feeding techniques, comparison of results from different sources must be judicious.

Differential feeding trials may also be combined with aims other than the determination of food attractiveness. For example Mulkern (1969, 1970) used the method to isolate phagiostimulant substances and to test the effects of plant extracts on grasshopper growth and development. Hewitt (1967) used it as a means of demonstrating plant resistance to grasshopper attack, while Abushama (1968a) combined choice experiments to observe the role of receptors on food selection.

Study of Crop and Faecal Contents

Introduction. This method relies upon the fact that the fragmentary plant material accumulating in the gut in a state of incomplete mechanical and chemical digestion contains identifiable fragments such as fibres, hairs, vascular tissue and in particular the plant cuticle. The cuticle is a morphological entity and forms the continuous outer layer on the shoots of green plants and is formed by the polymerization

of unsaturated fatty substances (Hercus, 1960). When cell growth is completed, the cuticle becomes hardened to a solid film, moulded to the contours of the underlying epidermal cells, of which the walls may also become impregnated. The cuticle is resistant to chemical attack, with the result that during digestion the cuticle, and in grasshoppers, usually the attached cells of the epidermis, remain unchanged apart from mechanical breakdown. The size, shape, differentiation, and distribution of epidermal cells and associated structures, such ashairs spicules, gland cells, intra- and extra-cellular deposits are characteristic for a plant species on a given part of the plant. Varying conditions of plant growth generally produce changes in the dimensions and distribution of these identifying charactersitics but their structure remains essentially the same (Metcalfe, 1960). Therefore reference cuticle specimens from plant species on the area over which the study is conducted may be used for the indentification of unknown material such as the ingestia of herbivorous animals.

Applications of cuticle analysis. The technique of cuticle or epidermal analysis has been widely applied in plant taxonomony (Davies, 1959; Metcalfe, 1963) and in investigations of the diet of higher herbivorous animals. For instance Dusi (1949) investigated the feeding habits of cottontail rabbits in Idaho, Martin (1954) of Scottish hill sheep, Storr (1961), and Stewart (1965, 1968) of game animals, and Ward and Keith (1962) used the technique in a study of

American pocket gophers. In New Zealand, cuticle analysis has been used in the dietary study of sheep (Croker, 1959; Hercus, 1960), the Australian oppossum by Gilmore (1967), and currently in the study of game animals (C.L. Batcheler and A.C. Christie pers.comm.).

This means of determining diet has had more restricted use in the determination of insect diet. Isely and Alexander (1949) suggested that fragments from grasshoppers could be utilized to investigate feeding habits. Mulkern and Anderson (1959) and Brusven and Mulkern (1960) developed practical techniques for the use of epidermal analysis in grasshoppers. This formed the basis of extensive investigations into the feeding habits of North Dakota grasshoppers in relation to their respective habitats in lucerne fields, sand hill prairie and prairie grassland by Mulkern and associate workers (1962, 1964 and 1969). In all, the technique was applied to many thousands of grasshoppers representing many of the 81 species represented in the fauna (Mulkern, 1969). Several very much more restricted studies have been carried out using crop analysis merely to define the broad feeding habits of the associated grasshoppers, by Kelly and Middlekauf (1961), Blackith and Blackith (1966), and Alexander and Hilliard (1964).

Cuticle analysis work in insects has largely been confined to grasshopper studies. This is possible because of the fact that fragments are sufficiently large for ready identification, and because feeding is very largely inflicted upon the leaf

lamina of plants, which most readily facilitates such an investigation. However, B.P.J. Molloy (pers.comm.) has used epidermal analysis to investigate the feeding behaviour of New Zealand porina caterpillars (Wiseana species) and W. Kain (pers. comm.) to investigate the feeding of adult grassgrub Costelytra zelandica in relation to dispersal. Batcheler (pers.comm.) is also currently investigating feeding behaviour of alpine grasshoppers of Cupola Basin, Nelson, by this means.

Advantages of cuticle analysis in insects compared with higher animals. Analysis of insect food by cuticle analysis is favoured to some extent over that of other animals by reason of the following:-

(i) Severity of digestion: Croker (1959) found in sheep that only mature tissues were likely to have survived digestion, and that more delicate cuticles of some species were found to be unidentifiable from the faeces. In grasshoppers, further breakdown of cuticular characteristics is slight after initial mastication, so that analysis from any portion of the alimentary canal and faeces is possible, although analysis of crop contents was found to be the most convenient by Mulkern (1967). Because of the less severe chemical digestion in grasshoppers, the cuticles ususally remain with the epidermis attached, also facilitating easier identification.

(ii) Size of individual specimens: subsampling of material is a necessary feature of work in higher animals, with the possibility of associated errors in quantitative and

qualitative work (Stewart, 1968). In grasshoppers the total contents of a grasshopper crop or section of gut may be observed on one microscope slide and every recognisable fragment identified. Furthermore, the size of individual fragments are of a size convenient for identification, and minimal preparatory treatment of samples is required.

(iii) Number of plant species represented in individuals: grazing animals ingest a wide range of plant species, both selected and accidental, when feeding. Because the cuticles of different species are broken into fragments of variable average size upon mastication, quantitative estimations of intake cannot therefore by gauged from frequency determinations alone. Stewart (1968) attempted to overcome this deficiency in the investigation into the diet of Kenyan game animals by multiplying the frequency of fragments by their dimension. A slightly less tedious method was employed, which also took the relative area of fragements into account, that of analysing the sample by point analysis on the slide. Because only one or a few species are usually associated with each grasshopper gut, identification of contents, and quantitative work is much more readily facilitated, permitting the fairly rapid investigation of large numbers of grasshopper specimens.

Advantages as a technique for grasshopper diet determination: Epidermal analysis has many advantages, both practical and theoretical, over other methods for determining grasshopper diet. Since specimens may be stored indefinitely, extensive collection of grasshoppers may be made at predetermined times, and when field conditions are suitable, with later analysis taking place in the laboratory. This facilitates the accumulation of adequate quantitative data to enable the derivation of sound, statistically based observations on feeding habit. The data obtained is free from external influence, and thus pertains directly to the field area at the time for which the grasshoppers w were collected. This fact, and the ready conversion of absolute data on ingestion into frequency form permits convenient comparison of grasshopper intake between collection sites, seasonal or daily collection times, and between grasshopper species, sexes and instars.

However, in order to fully interpret feeding results obtained for grasshoppers, it is necessary to supplement this data with information on other aspects of feeding and non-feeding behaviour, determined from direct observation. It is also necessary to determine the relationship between the frequency of ingestion of plant species, with their abundance in the vegetation, before proper conclusions on feeding selectivity can be drawn.

Quantitative expressions for describing food habits: Most of the work on grasshopper diet is of a qualitative nature with regard to food intake. However Mulkern et al (Mulkern, 1967)

have derived several expressions for the description of grasshopper diet. The unwritten assumption that the quantity of each plant species ingested relates directly to its frequency of occurrence in the gut is valid in most grasshopper species analysed by them (Mulkern et al, 1962, 1964, 1969), since each crop generally contained one plant species only. The quantitative intake of plant species may be necessary to define accurately the role of grasshopper feeding on individual components of the vegetation, particularly in multiple feeders. Quantitative expressions included:

(i) Grass forb index (GFI) in which the percentage of grasshoppers of a species containing monocotyledons in their crops was subtracted from those containing forbs. Five groupings were then classified on a scale between 100 (forb feeders only) and -100 (grass feeders only).

(ii) Plant specificity index (PSI). This was used to determine the relative degree of diet restriction between grasshopper species. The highest ingestion percentage of a plant species in the diet was multiplied by three, the second by two and the third by one, the sum of these being divided by three. Figures close to 100 indicated marked selectivity, while greatest diversity of feeding was indicated by figures of around 20.

(iii) Plant value index (PVI) was determined as a multiple of the ingestion of plants and their value as stock forage. This expression was devised to compare the

importance of grasshopper species as competitors with stock. The expression is therefore of little application in New Zealand alpine situations where vegetation is considered in terms of its contribution to conservation rather than stock production. However a similar expression could be devised to relate feeding of grasshopper species to this function of the vegetation if a value of conservation was derived for the plant species.

(iv) Relationship between plant ingestion and abundance in the vegetation. Plants ingested at a rate lower than their abundance indicated an avoidance or lack of preference for them by grasshoppers. A level of ingestion approximating its abundance indicated acceptability or some degree of preference, while those plants ingested at a rate above the abundance indicated a preference probably requiring the seeking of it for consumption by the grasshoppers.

The techniques involved in cuticle analysis are discussed under Experimental Methods in Chapter 5.

6 SOME FEATURES IN THE ECOLOGY OF ALPINE GRASSHOPPERS

Composition of Alpine Faunae

Although ecological work on alpine grasshoppers is very restricted, it is apparent that the New Zealand fauna is unique in several aspects. Alexander (1951) noted that at high

altitudes in Colorado, Acrididae both as species or as individuals were among the most numerous insects. But of these only 39% (11 species) were resident, the remainder being accidentals occurring as fully winged adults which bred below timberline (Alexander, 1964). Uvarov (1952) also found that only a small proportion of species (4/33) found on Mt.Egan, East Africa, were truly alpine. Similarly in the North West Himalayan region, some 40% of all species were found above timberline, of which only three percent were true mountain forms (Mani, 1962). In contrast, as mentioned earlier in the review, almost the entire New Zealand fauna consists of eualpine species.

Other Characteristics

Mani (1962) found that the Himalayan alpine species were all diurnal and flightless, being either apterous or brachypterous. These features also characterise the New Zealand grasshoppers. However the life cycle appears to have become adapted to the alpine climatic environment in a different manner. Mani (1962) noted the presence of an annual life cycle, with diapausing egg stage in the Himalayan species. The life cycle of Aeropedellus clavatus, also annual, was found by Alexander and Hilliard (1964) to be adapted to the Coloradan alpine environment by being very abbreviated. Egg hatch occurred immediately after snow melt. It was noted that egg deposition occurred in the bases of tussocks in this species,

rather than in soil as is conventional. With the passage of four immature stages, adults appeared only six weeks after egg hatch. In contrast to this, New Zealand Acrididae are adapted in the other extreme, with a prolonged life cycle lasting several seasons and including at least six instars. This feature was considered by Batcheler (1967) to be an adaptation in response to the variability in the climate. Under a strong oceanic influence, the winter temperature minima as observed by Morris (1965) in the Craigieburn Range, Canterbury, appeared to be warmer than in Continental alpine areas. This resulted in an erratic period of winter snow cover. In addition to this however, daily temperature variations were high and frost could be expected in any month. This predescribed the necessity for flexibility in the grasshopper life cycle, with a degree of cold temperature tolerance in most if not all instars. In this respect a possible hibernating rather than diapausing behaviour in hoppers after egg hatch, affords the grasshoppers optimal use of any climatically favourable periods for activity and development.

Implication of New Zealand Natural History in Present Day Grasshopper Distribution

When considering the above features of the New Zealand grasshopper fauna, it seems that reasons other than the mere immutability of cold temperature tolerances, acquired during the glacial periods, are necessary to explain their present

restricted diversity and distribution. Such a view was also expressed by Dumbleton (1970). Explanation is best found in terms of the environmental requirements of grasshoppers, and changes occurring as a result of geological and climatological history. These may be exemplified by the changes since the end of the Ice Age epoch. Following this era, the last glacial retreats of which occurred some 15,000 years ago, the vegetation of the South Island is thought to have advanced from ice free refugia (Wardle, 1963). Pollen evidence of Cranwell and von Post (1936) indicated a subsequent succession of three climatic periods, with associated floristic biomes. A severe post-glacial period was marked by extensive grassland vegetation, followed by an equable warm moist period favouring the development of forest. This period, the zenith of which occurred some 5000 - 3000 years ago, was also the period of optimal development of alpine soil and vegetation (Molloy, 1964). This period was followed by climatic reversals, giving rise to the present cooler, drier regime, and contributing to the present superficial features of scree slopes, pedestalled vegetation and solifluction terraces in alpine areas (Molloy, 1964) and present altitudinal limits of vegetation zones (Raeside, 1948; Holloway, 1954). Throughout this period of its development, the vegetation was without the influence of man, or of foraging animals, with the exception of birds, most notably the Moa.

The open grassland habitat required by grasshoppers has in other parts of the world been maintained to a large degree by

the influence of climatic aridity, grazing herbivores or fire (e.g. Reigert, 1968; de Vos, 1969). New Zealand vegetation has been under the influence of man only in the last millennium (Suggs, 1962), with a much briefer period in the presence of grazing mammals. In the absence of the direct and indirect consequences of these factors, especially that of fire, vegetation cover could have been both effective and stable. Suitable habitats for grasshoppers would then have been at a premium, particularly during the equable period. The alpine area was marked by soil accumulation in this time. The comparative absence of a wasting regime resulted in watershed stability, with the result that riverbeds in lowland areas would also be densely vegetated to the water's edge. Enclaves of grassland within an almost exclusive cover of forest below timberline, were probably insufficient in size and quality to maintain grasshoppers. During this time the grasshoppers probably became restricted to alpine areas, the only region where, as a result of the inherent instability of the country, geological erosion, and the extent of natural grassland vegetation, grasshopper populations could be perpetuated. Because of the high degree of physiological specialization required by insects to exist in these environments, (Mani, 1962), the occurrence of extensive genetic readjustments would be required to enable a reinvasion of lowland areas. The time that has elapsed since other environmental conditions have become tenable for grasshopper occupation in these locations

have obviously been insufficient for such changes to have occurred.

Such an hypothesis helps to explain the peculiarities in the New Zealand Acridid fauna, in particular the overall deficiency of species, and very restricted lowland and North Island faunae. Also the absence of a strongly developed Australian affinity in the fauna, when circumstances of prevailing winds and the winged habit of many lowland grasshopper species (e.g. Phaulacridium) would seem to suggest a predisposition to immigration of such faunistic elements, is also explained in the absence of suitable conditions upon their arrival in New Zealand.

Implications of Recent History in Present Grasshopper Populations

After the arrival of man in New Zealand, burning by Polynesians had the first major impact on the structure of vegetation. The effect of burning imposed on vegetation which was adjusting to a reversal from the optimal climate was apparently dramatic. Tussock cover was opened, much erosion was initiated and grassland was extended into many areas formerly occupied by bush (Molloy et al, 1965; Molloy, 1967). This situation was later aggravated by the more extensive burning after the arrival of Europeans, together with the interaction from concurrent grazing by introduced animals. These circumstances had the greatest influence in the mountain areas

east of the Main Divide and between the Waitaki River in the south and Wairau River in the north. Characterised by steep slopes and mechanically unstable soil and scree product derived from greywacke parent material, the result was the subsequent extensive development of erosion.

However these changes which were inflicted on the vegetation were largely of a nature favourable to aspects of grasshopper food/shelter and reproductive environmental requirements as detailed earlier in the review. The opening of the climax grassland vegetation has enabled an increase in the availability of minor, more succulent plant species generally favoured by grasshoppers. The open sites have created more favourable situations for the other aspects of the daily behaviour regimen, whilst maintaining dense cover essential for shelter. Finally an increased exposure of bare soil improved the opportunities for egg rearing. It would therefore be of little surprise that grasshoppers may have increased to levels at which they have some influence in the present and future status of the vegetation, and which certainly justifies the investigation of their ecology.

CHAPTER 3

THE STUDY AREA

LOCATION

The field area for the present investigation consisted of two adjacent upper catchments of the Broken River and their associated ridgetops. The area is contained within State Forest 22, a protection forest and forest park located to the northern end of the Craigieburn Range, and approximately 70 miles east of Christchurch on the main Arthurs Pass and West Coast highway.

Broken River is a middle order tributary of the Waimakariri River, and drains eastern slopes of the Craigieburn Range. This range forms the south-western boundary of the Upper Waimakariri basin, and together with the Black Range, divides it from the Rakaia catchment to the south. Of the two catchments used in this study, Alan's Basin has a general south easterly aspect, backing onto the main Craigieburn axis and rising to just over 6000 feet in altitude.

Camp Stream on the other hand is headed by a subsidiary ridge which separates Broken River from the Craigieburn River catchment, and it experiences a southerly aspect.

The topography and watershed condition of the area is typical of much of the high country situated east of the Main Divide between the Waitaki and Wairau Rivers. It is characterised by the presence of steep slopes, areas of highly modified vegetation and extensive scree development.

The forest park forms a mountain lands study area for the Forest and Range Experiment Station, Rangiora. It presently supports wide ranging investigations into the meteorological, hydrological and ecological aspects of the high country environment, with particular emphasis on the revegetation of eroded and depleted areas. An extensive review of the natural history, and of scientific investigations pertaining to the upper Waimakariri area appear in "The Waimakariri Catchment" compiled by Hayward (1967).

The two basins were selected in the present study for the following reasons:-

(i) The proximity to Lincoln College, and accommodation by courtesy of the Forest and Range Research Institute, and ready access to alpine grassland areas.

(ii) The good range of potential grasshopper habitat types were available.

(iii) Other investigations, particularly climate

studies being carried out in the area were of relevance to the study.

(iv) Both basins were free from ski club activities.

PHYSICAL FEATURES

Climate

The area has been under intensive climate investigations since 1961. Data for the 1961-63 period was reviewed by Morris (1965), while meteorological data for seasons more relevant to the present study appeared in unpublished reports compiled by Apse (1967, 1968, 1969). Four of the meteorology stations established in the area were of direct relevance to the present study. These were sited on Alan's scree, designated AO, altitude 4200 feet, Ski Basin (SB) 5000 feet, Nervous Knob (NK) 6000 feet and Camp Stream (CS) 4700 feet.

Temperature. As the Craigieburn Range is no more than 60 miles east and west of the Pacific Ocean and Tasman Sea respectively, the climate is under a moderating oceanic influence. As a result seasonal temperature ranges are low by continental standards, and are characterised by a warmer winter minimum (Morris, 1965). Furthermore the prevailing northwest wind is somewhat under rainshadow influence from the Southern Alps. These factors prevent the accumulation of deep lying

snow. The winter snow cover is therefore erratic though may be continuous between May and November above 5000 feet. The winter snow cover provides an unreliable protective mantle for plant and insect life and exposed ground surfaces against frost.

Despite the low seasonal range experienced, diurnal temperature variations are high and frosts may be expected in any month. Camp Stream station experienced about 110 screen frosts per year, during the period of climate studies, while the Ski Basin site recorded 160 in 1962 and 192 in 1968. Freezing was likely to occur at a depth of two inches on bare ground in at least six months of the year above 4000 feet. Drastic effects on new vegetation growth caused by heavy unseasonal frosts were considered possible by Morris (1965).

Growing Season. Morris (1965) estimated the growing season from the number of days in which the temperature mean exceeded 42 degrees Fahrenheit. This gave a growth period of 120 days at 4700 feet and 100 days at 5000 feet. Benecke (1968), using exotic tree species, found that the growth period was also dependent on the phenology of plant species. That of Alnus viridus was found to be controlled by photoperiod at outset and culmination, and was therefore approximately constant with altitude, measuring 140 days on scree at 4200 feet. In Pinus Contorta, bud initiation appeared to be regulated by temperature, with the termination of growth under photoperiod control. This resulted in a growth period of 86 days at

4000 feet and only 47 at 5400 feet. In both species the actual amount of annual new growth was markedly influenced by the temperature of different altitudes even after allowing for other site differences.

Precipitation. Annual precipitation rose with altitude and was about 70 - 80 inches above 4000 feet (Morris, 1965). Some 30% of the annual precipitation was found to fall as snow above 5000 feet, while there was a rapid decrease to 20% at 4700 feet (Morris and O'Loughlin, 1965). The monthly distribution of precipitation was even, although periods of high intensity rainfall occur occasionally. As monthly rainfall exceeds that of monthly potential evapotranspiration, water deficits were not considered to be a factor of importance limiting vegetation growth. (Morris, 1965).

Wind. Wind intensities are generally high in the area though the effects of topography and wind channelling are also quite marked. The average mean daily wind run averaged 120 miles at 5000 feet, with the monthly average of daily wind speed varying from three to seven miles per hour (Apse, 1967). This compared with only 29 miles mean daily wind run at 3000 feet. The wind is an important factor in alpine environment, influencing soil loss and plant growth. The abrasive effects of windblown snow particles is particularly marked in exposed situations in the Craigieburn Range where snowcover is frequently not deep enough to cover the vegetation. Information is not available regarding the influence of wind as opposed to temperature

effects on plant growth.

Influence of climate on grasshopper bionomics. General climatic data is useful only in determining broad influences on grasshopper behaviour since microsite variations are likely to be very large, especially at the ground levels which grasshoppers occupy. Fisher (1952) and Benecke (1968) showed the tremendous range, and rapidity of fluctuations, in temperature to be found on scree surfaces compared to vegetation. Shading of the sun by cloud alone produced a drop of 30 degrees Centigrade on exposed scree (Fisher, 1952). Differences in temperature between scree and vegetated sites extended up to fourteen inches in depth.

Of the climatic factors affecting grasshopper bionomics, temperature undoubtedly has the greatest direct influence on the activity of grasshoppers. In this regard New Zealand grasshoppers appear to have a great seasonal flexibility and generally appear to be active in snow free conditions as long as the air temperature is sufficiently warm, above about 50 degrees Fahrenheit. The low grasshopper activity levels observed under cloudy, windy or rainy conditions is probably the result of low temperatures coincident with these factors. Wind is a particularly important factor in the Craigieburn Range, greatly reducing activity in otherwise favourable conditions. Wilson (1959) noted that the cooling effect of wind was particularly marked in alpine areas, especially in sunny conditions. He also commented on the efficacy of tussock vegetation as a

windbreak at ground level, noting that windspeed in the lee of tussocks was only about ten percent of that above vegetation.

The intraseasonal variability in climatic conditions in New Zealand mountains have probably necessitated the flexibility in the life cycles of the grasshoppers. The seasonal variability, particularly with regard to overall temperature conditions and length of snow lie, must also influence directly the total activity and hence cumulative feeding damage that can be inflicted over a season. Altitude also influences the total period of time in which grasshoppers may be active. However, the reduced vegetative growth in response to increased altitude probably means that grasshoppers become a critical factor in the vegetation at lower population levels with increasing altitude. The unseasonal frosts, and the unreliability of winter snow cover imply that eggs and all other stages have a degree of frost resistance that is not seasonally controlled.

Soils

Nordmeyer (1966) quoted unpublished work by Kelland who recognised four main soil types in the Broken River Basin. Two of these were skeletal, and the other two were related steepland complexes of the high country yellow brown earth group. These included:

(i) lithosols - soils developed under scattered rock crevice plants and lichens on rock barrens at the top of

ranges.

(ii) alpine soils - developed under scree.

(iii) Tekoa steepland soils - formed under beech or former beech forest.

(iv) Spencer steepland soils - developed under snowgrass vegetation.

Characteristics of the major soil types were presented by Hayward (1967, Chapter five and Appendix). The Spencer soil is closely related to the better known Kaikoura type, though developed under higher rainfall. The Spencer soil is weakly weathered, moderately leached and texture is characteristically of sandy loam type. It is generally free draining, though poorly supplied in available nutrients, particularly the subsoils. The organic matter content is low, but of a high C:N ratio that indicated a somewhat raw state (Nordmeyer, 1966). The weak crumb structure and friable condition predisposes exposed soil to severe frost movement, with subsequent sheet erosion and scree formation. The poor nutrient status of the soil imposes limitations on the production of vegetation, which together with the harshness of the climate render it very susceptable to deterioration in the presence of added stress factors e.g. fire, stock and perhaps insects.

Vegetation. Lower slopes in the area are dominated by mountain beech forest (Notofagus solandrii var. cliffortioides). The bushline at about 4500 feet formed the lower boundary in both catchments for the present study. A very poorly developed

scrub zone is present locally above the beech forest, consisting largely of sparse bushes of mountain totara (Podocarpus nivalis). However alpine snow tussock grassland is the principal vegetation type above bushline. Where not penetrated by extensive slopes of mobile scree, the grassland vegetation forms dense to open cover to an altitude of 5500 feet. At its upper limits the vegetation gives way to the scattered plants on scree debris and rocky bluffs. The presence of remnant and pedestalled patches of typical tussock vegetation extending to the ridgetop at 6000 feet are suggestive of the former higher limit of continuous vegetation as postulated by Raeside (1948). The extensive mobile scree slopes frequently extend to the foot of the slopes on which they occur (Plate 1)

The tussock vegetation is dominated by the midribbed snow tussock Chionochloa pallens. The upper Broken River area in which the study was conducted, forms the eastern-most extremity for the distribution of this species before being replaced by C.rigida as the dominant species (Wraight, 1967). This transition corresponds approximately with the fifty inch rainfall isohyet (Burrows, 1967). The latter species and also C.macra, are present in the study area in some mixed and pure stands, and may also form hybrids with C.pallens.

Where fire and grazing by ungulates has resulted in a strongly modified sward, species of Celmisia, particularly C.lyallii become major constituents, to the extent of becoming

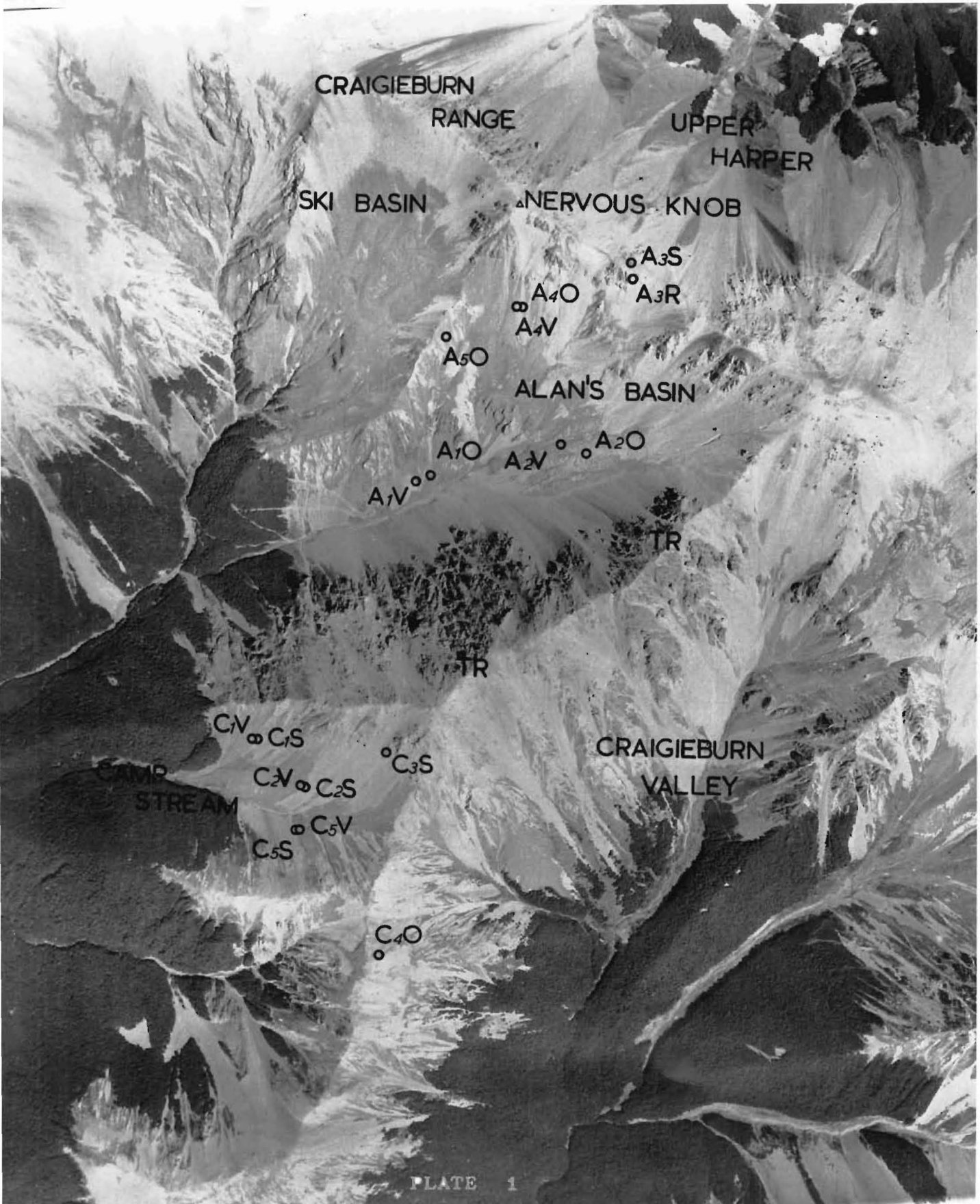


PLATE 1

Aerial Photographs of part of the Upper Broken River Catchment Craigieburn Range, indicating locations of Plots used in this Study

co- or subdominant with Chionochloa pallens. The flora of minor species is rather varied between stands in the area, and total in excess of 130 species (Chapter 4).

In more specialized local situations other species share or assume dominance with C.pallens as follows:-

(i) Chionochloa crassiuscula may form a dodominant with C.pallens in Alan's Basin between 5000 and 5500 feet, but becomes dominant on the upper edges of snow hollows in this Basin.

(ii) Chionochloa oreophila occupies the floor of snow hollows in Alan's Basin forming a low mat cover.

(iii) Dracophyllum pronum frequently provided the dominant ground cover on rocky sites on or near the ridgetop, and on other exposed stabilized scree and solifluction terrace situations.

(iv) Rostkovia gracilis became dominant in moist shady areas and around seepages.

General Condition of the Vegetation

The report on the Waimakariri catchment (Hayward, 1967) revealed, among its other conclusions, that knowledge on the trends in plant cover and erosion under past and present circumstances was inadequate. Molloy (1967, p.66) noted that the most spectacular erosion in the Waimakariri catchment lay in the zone of Polynesian burning, an area which today roughly coincides with that grazed by sheep. The findings of Wraight

(1967, p.75) lend support to the implication of sheep in continued deterioration, where it was noted that the condition of alpine and upper montane grassland in this region was generally poor and frequently showing a downward trend in condition. Wraight (1967) attributed this largely to the continued grazing by domestic animals. As an exception to this, the swards surveyed in the Craigieburn Forest area, which have been under a regime of rigorous control of deer and chamois, and discontinued sheep grazing, were in better condition and showing upward trends in condition. This situation was also reflected in the marked improvement in the condition of beech forest in this area (Holloway and O'Loughlin, 1967). In the higher rainfall areas of the catchment and beyond the zone of Polynesian burning, the survey indicated a mixed trend in condition of swards from stationary to good improvement. Curtailment of further extension of large scale deterioration was regarded as a favourable response to the successful control of wild animals in the area (Wraight, 1967).

Wraight (1967) considered that many of the swards in poor condition would not show a reversal in downward trend merely by relief from grazing pressure, but that these would require re-vegetation by artificial means. Although not included in the survey by Wraight, swards in such condition are present in the Craigieburn Forest area and were included in the present study. It was observed in the literature review that such open sites generally favoured grasshoppers. This

therefore bears the implication that grasshoppers in the New Zealand alpine areas occur in greatest numbers on swards which are least able to carry them. This increases the possibility that grasshoppers could be aggravating the downward trend in condition in poorly vegetated areas.

CHAPTER 4

METHODS AND MATERIALS

SCOPE OF INVESTIGATION

The overall objective in the study of applied entomology in natural environments should be seen as the determination of the role of insects in, or impact on, the vegetation. Necessarily more specific in its aim, the present study involved the determination of feeding habits of grasshoppers in an alpine area. Such a determination was a necessary preliminary towards the major objective, by enabling an indication of the direction and type of damage which may be inflicted by grasshoppers. Batcheler (1967) has already indicated that grasshoppers could be exerting an unfavourable influence on the vegetation in some situations in alpine areas.

A survey of the literature (Chapter 2) revealed that food selected by grasshoppers in the field was greatly influenced by its availability in the vegetation. Thus in order to gain an

indication of the impact of grasshopper feeding on the vegetation it was necessary to determine the diet of grasshoppers under natural conditions, and to relate these findings to the abundance of the plant species in the vegetation. Furthermore it was revealed in the review of literature that although not generally of greatly restricted feeding habits, grasshopper species showed definite feeding preferences to varying degrees. As a consequence, it was considered necessary to determine the pattern of food selection of the four grasshopper species in the study area, in order to obtain an accurate indication of the role of the grasshopper population as a whole in the vegetation. As a secondary aim some insight could then also be gained into the interspecific differences in food selection patterns, with subsequent implications as to the nature of competition for food by sympatric populations, reflected in the degree of food specialisation developed.

The above characteristics of grasshopper food selection inferred that two major aspects of study would be required in the present investigation.

(i) Analysis of the vegetation associated with the grasshoppers.

(ii) Determination of the feeding habits and preferences of grasshoppers with respect to the analysed vegetation.

The necessity of interrelating the results of these separate

aspects in each case influenced the method of analysis most applicable. Determination of the frequencies of plant species present in the vegetation, and of those ingested by grasshoppers, most readily facilitated such an analysis. Point analysis of the vegetation was used in the determination of vegetation frequency, while the determination of food selection in grasshoppers was determined largely from analysis of gut contents. The analysis of grasshopper diet was of a qualitative nature, based on the occurrence of plant species in grasshoppers.

A. ANALYSIS OF VEGETATION

Introduction

The plant ecologist is interested in measuring the parameters of cover, density, frequency, yield, etc., principally to determine trends in the floristic composition, structure, or production of vegetation over space and/or time. The techniques available for such analyses are largely reviewed by Brown (1954). Many of the studies in New Zealand tussock and alpine vegetation were reviewed in "Methods and Measurement of Plant Communities" (1962), a publication by the New Zealand Institute of Agricultural Science. Many of these investigations were designed to determine trend in vegetation cover (Wraight, 1962; Hercus, 1962) and used specific

frequency determinations from various adaptations of the quadrat technique. In phytosociological studies, Billings and Mark (1961) and Daly (1966) have employed the point analysis technique developed by Levy and Maddon (1933).

The present study required a quantitative, in situ analysis of the vegetation, the results of which not only enabled comparison between various plots analysed, but also between the diet selected by grasshoppers within these plots. Point analysis provided the most adaptable method for gaining such a representation of the vegetation composition. The point, actually the ultimate reduction of a quadrat, enabled a determination of the absolute frequency of species in the vegetation, and also an estimation of the cover. The technique therefore provided a frequency value with which ingestion may be directly compared, as well as an indication of the value of a plant species in soil protection.

Analysis of the vegetation was conducted in plots representative of areas over which the grasshoppers were collected for analysis of gut contents. Field work on the vegetation was carried out over the summer months of 1968/69 during which the bulk of grasshopper specimens were also obtained. For easier description, the work on the vegetation is divided in this Chapter into three sections as follows:-

(i) Plot location

(ii) Qualitative analysis of plot vegetation

(iii) Quantitative analysis

Plot Location

After a general reconnaisance, five locations were selected in each of the two study catchments to include a range of habitats occupied by grasshoppers, with respect to topography, aspect, and in particular, structure and composition of vegetation. The locations were chosen for their uniformity in these respects over a sufficiently large area within which to collect grasshoppers for diet analysis. Within each location, one to three plots each of $\frac{1}{2}$ square chain area were located by corner pegs and representing different habitat types occupied by grasshoppers in the area. The vegetation was analysed within these plots, while grasshoppers were collected from within and immediately surrounding these areas. It was therefore assumed in comparing grasshopper diet with vegetation data, that grasshoppers had selected their diet in the area in which they were sampled. Observation in the field indicated that this assumption was in most cases valid.

In general the occupation areas of the grasshoppers were observed to be divided into three general types of habitat as follows:

(i) Closed vegetation, away from scree areas. These sites had a high proportion of ground area covered by vegetation, with little exposed soil and little or no erosion pavement or scree development. These sites were occupied by Paprides nitidus and Sigaus australis only. Numbers generally decreased as the vegetation became more dense and rank.

S.australis appeared to be less tolerant of dense, tall cover than did P.nitidus.

(ii) Closed vegetation bordering onto scree. These sites were of similar vegetation composition to the above, but with an abrupt demarkation between vegetation and scree areas. Such sites were provided by a narrow border zone between continuous vegetation and scree, or by isolated patches of remnant vegetation that were surrounded by coalescing scree areas. These areas were frequented by Brachaspis nivalis in addition to the other two species above, and also by S.villosus at sufficiently high altitudes. It was observed that B.nivalis generally did not penetrate more than a few yards from the scree verge into continuous vegetation.

(iii) Open vegetation interspersed with erosion pavement and scree surfaces. These sites were present where the vegetation had been seriously modified by erosion induced in deteriorated vegetation, or on outwash fans where vegetation was being, or had been partially overwhelmed by accumulating material. On these sites the tussock plants were sparse, with a large proportion of intertussock area not covered by vegetation. In these areas the three main grasshopper species occurred sympatrically. Typical sites in these categories are depicted in Plate II a, b, c.

In total, seventeen plots were established from the ten original locations. In most cases these plots were of 1 chain by $\frac{1}{2}$ chain, pegged up and down the slope. However the scree

a. Plots C2V and C2S Dense Vegetation and Dense Vegetation bordering onto Scree

b. Plot A3S Remnant Patch of Dense Vegetation

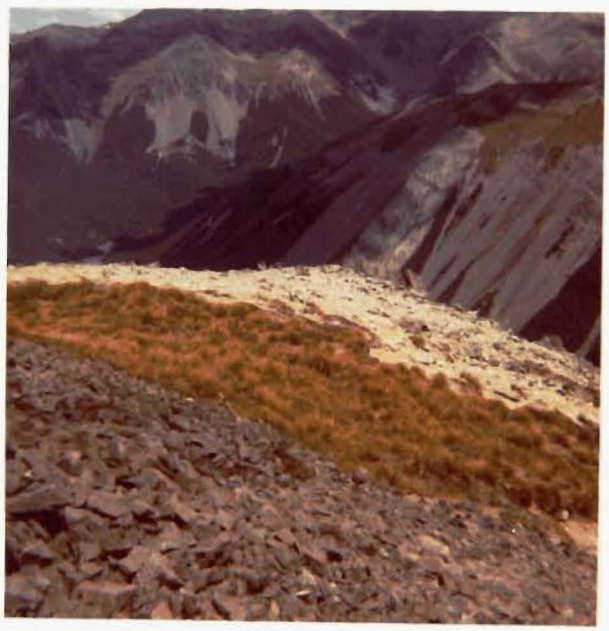


PLATE 2

Typical Vegetation Cover on Plot Types used in the Study

c. Plot C50 Open Vegetation interspersed by erosion pavement

d. Plot A3R Rocky Bluff Habitat occupied by Sigaus villosus

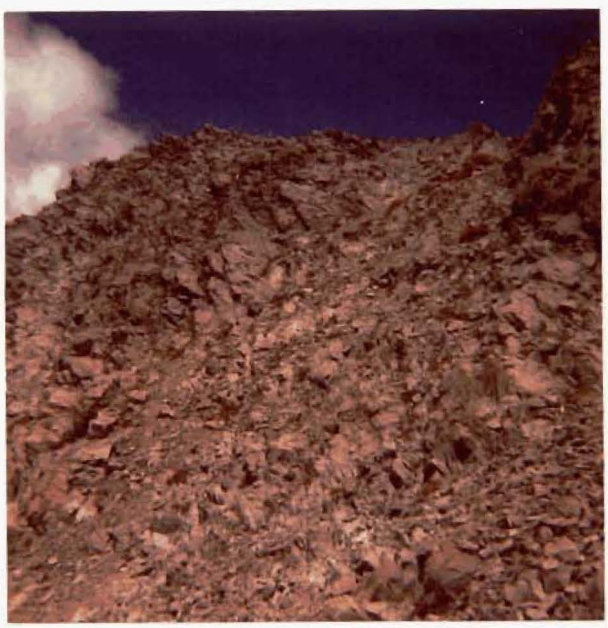


PLATE 2 (cont.)

verge plots were measured at 2 x $\frac{1}{4}$ chain, lying up and down the scree verge. This was done so that the vegetation analysed corresponded with the area from which B.nivalis selected its food.

Each plot is designated symbolically thus:-

Prefix referred to the catchment location

C = Camp stream

A = Alan's basin

The numerals 1-5 referred to locations within a catchment

Suffix referred to the habitat type referred to above

V = continuously vegetated sites

S = scree verge

O = open sites

Thus C1S, A5O, etc.

The location of plots are marked on the aerial photograph of the study area (Plate I) and individual descriptions are given in Table I and pp. 82 -86.
In addition to those areas upon which the vegetation was analysed, grasshoppers were also collected from two areas to enable the determination of diet for S.villosus. This species occurred sparsely, with B.nivalis, among the very scattered vegetation at high altitudes and were therefore insufficiently represented on other plots. One of the collection areas consisted of the whole top ridge dividing Alan's Basin from

the Craigieburn Valley (designated TR). The other site consisted of a rocky bluff located near A3S, designated A3R and depicted in Plate II, d.

Owing to the orientation of the Craigieburn Range, most plots lie in the easterly sector. One location for each catchment was selected to represent an exposed northwesterly aspect. These were located near the head of each basin and actually drained into the respective catchments adjacent to these two basins. Altitudes ranged from 4400 feet to 6000 feet, with most plots in the alpine grassland belt between 4500 and 5500 feet. The slope of most plots lay between 20 and 33 degrees from the horizontal. These features are summarised in Table 1.

Qualitative Analysis of Vegetation

Plant taxonomy. To facilitate the quantitative analysis of vegetation, and the identification of plant species recovered from grasshopper guts, a floristic list of all plant species located in or near each and all plots was assembled. Presence of a plant species in association with plots was ascertained during a systematic search of the area, and as a result of point analysis, and grasshopper sampling on the plots.

Identification of unfamiliar plants was made in comparison with Lincoln College Herbarium specimens. Confirmations of all identifications were made from literature sources as follows overleaf:

Plant Species	Source
Indigenous dicotyledons and Pteridophytae	Allan, 1961
Exotic Compositae	Healy, 1962
Chionochloa species	Zotov, 1963
Chionochloa macra Zotov	Zotov, 1970
Luzula species	Edgar, 1966
Astelia nervosa Hook.f.	Moore, 1966
Other monocotyledons	Cheeseman, 1925
Polytrichum juniperinum Hedw.	Sainsbury, 1955

The full floristic list appears in Appendix A. In most cases the notation used was drawn from Burrows (1969), or from the appropriate source above.

Voucher specimens of most species were mounted and are deposited in the Lincoln College Herbarium. In addition, leaf specimens of all species were stored in tubes of botanical FAA solution, for preparation of plant cuticle reference slides used in the identification of grasshopper gut contents. The collecting began early in the 1968/69 summer season, although flowering specimens were added to the pressed and preserved specimens where possible.

In all, in excess of 140 species were represented, which consisted only of plant species located in or near plots.

TABLE 1

Summary of Plot Features, and Frequency Composition of Cover in the 19 Plots Sampled in the Craigieburn Range Study Area

Plot	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	A3R	TR
Altitude (ft)	4600	4600	4700	4700	5300	5000	4700	4700	4400	4400	5000	5000	5050	6000	5300	5300	5150	6000	6000
Aspect	SE	SE	ESE	ESE	ESE	NW	SW	SW	NE	E	SSE	SSE	SSE	NW	ENE	ENE	NE	NE	-
Slope (°elevation)	33	33	31	31	37	23	33	33	25	25	21	21	21	18	30	30	28	43	-
Bare Ground (%)	1	12	2	25	16	28	1	7	8	32	1	5	29	20	9	40	34	-	-
Litter Cover (%)	5	7	5	4	5	6	3	2	11	4	14	5	1	9	24	17	12	-	-
No. of Species (Min.)	52	63	57	54	42	60	48	52	44	62	56	55	53	44	24	26	32	30	58
Composition of Cover (%):-																			
MONOCOTYLEDONS																			
Agrostis dyeri		*	*	t					*	*									
Agropyrum ensyii	*	*																	
A.scabrum	*	t				*				t									
Anthoxanthum odoratum									*	t									
Astelia nervosa											*	*	*	t		*			
Chionochloa crassiuscula											6	16	*	*	9	2	t		*
crown											2	2			6	t			
litter											2	2			5	t			
C.flavescens					*	*			t										
C.oreophila												22		*			*		
C.pallens: canopy	54	31	20	13	12	23	27	17	40	11	22	4	2	7	15	12	14	*	*
crown	11	5	4	2	3	4	5	3	11	3	8			5	6	5	4		
litter	4	4	1	3	1	1	2	1	8	2	8	t		1	5	5	3		
Deyuxia avenoides		*				*				t							*		*
Erythranthera pumila		*							*										
Festuca rubra						t			*										
F.novae-zealandiae		t	t			4									t	t			
Hierochloe fraseri	*	t			*														
Koelaria kurtzii		*			*												*		*
Lachnagrostis fosteri	1	1	t	t	1		1	1	1	*	t	t	*		t	t	1		*
Luzula pumila			*	t		*					t	*	t	*			*	*	*
L.rufa	*	t	t	t	*	2	1	2	*	1	1	*	t	*	t	*	*	*	*
L.traversii			t	t	t														
Microlaena colensoi			*	*			t	*	*	*	t	2	*						

Table 1 (cont.)

Plot	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	A3R	TR
Notodanthonia settifolia	*	t	*	*	3	*			t	1	*		*	3	2	t	11	*	*
Poa colensoi	10	10	5	7	16	9	7	8	1	3	7	6	3	11	4	7	6	*	*
P.mackayi	t	1	1	t			t		2	t	*			t	1	t			*
P.sclerophylla		*			*	*				*			*				*	*	*
Rostkovia gracilis	*		*						1		2	7	*	1			*		*
Uncinia sp.	1	*	*	t	*	1	1		*		*	t	*	*	1	*	*	*	*
Trisetum youngii	1		t						t		*	*							
DICOTYLEDONS																			
Abrotanella caespotosa				*															
Acaena spp	*	1							*	*									
Aciphylla squarrosa	*	t	*	*		t	t		4	1									
A.carnulosa								*											
A.monroi	*	t	*	*	9	t	*	1	*	1	3	2	1	2	4	2	1	*	*
Anisotome aromatica	1	4	9	2	1	1	14	10	*	5	6	9	4	1	*	*	3	*	*
A.filiforme	*	*	*	t	*				1	*									
A.pilifera																			*
Brachycome sinclairii	*	*				*				*		*	1						*
Cardamine spp.	t	*	*	*	*		t	*	*	*	*	*	*	*	*	*			
Celmisia discolor				*			*	*				*	*						
C.dubia												*	2	*					
C.durietzii	*	1					*	t				*		*					*
C.gracilenta						*													
C.laricifolia					*		t	2				4	2	2	t		*	*	*
C.lyallii: canopy	14	19	11	26	24	t	7	1	17	2	6	2	t	24	20	10	14	*	*
crown	1	1	1	1	1		1		1					2	2	t	2		
litter	t	1	1	1	1				1					2	8	3	3		
C.sessiliflora											*	2	1						
C.spectabilis:canopy	*	*	8	t		12	4	5		7	2	1	1	1				*	*
crown			1			1	1	t		2									
litter						1				t	t								
C.traversii												*							
C.viscosa: canopy	*	*	10	1	3	1	13	9	*	t	15	10	1	5	t	4	2	*	*
crown			2		1		1	1			2	1		1		t	t		
litter			1		1						1	1		1		1	t		

Table 1 (cont.)

Plot	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	A3R	TR
Cerastium vulgatum									*	*									
Colabanthus acicularis						*			*	t				*				*	*
Coprosma cheesmanii			t	*		*	*	1		6	*	2	*						*
C.pseudocuneata			*	*			*	*		2			t						
C.pumila			6	1	*	*	*	6		*	*	*	1	*					*
Cotula atrata		*						*											*
C.pyrethrifolia	*	2			*	*	*	*	*	2	*	*	*	*					*
Craspeda lanata																			*
Cyathodes colensoi						*													
C.fraseri						2													
C.pumila						*													
Dracophyllum pronum	*	1	3	t	4	1	6	20		*	6	*	34	5	*		*	*	*
D.uniflorum			*	*		*	*	*											
Drapetes dieffenbachii		*	9	*		*	t	t			4	4	2	*	*	*		*	*
Epilobium crassum		*				*		*											*
E.pedunculare	*						1			t	*	1							
E.perplexum	1	2	t		1		*		1	*							*		*
E.pycnostachium						*		*											
E.rubromarginatum	*	t	*	1	t	2	*		t	t				*		*	*		*
Euphrasia spp.	*	t	1	*		t	t	t			*	*	1						
Forstera tenella			*	t			*	t			*	*							
Galium perpusillum	*	1																	
Gaultheria crassa									*										
G.depressa	7	5	8	6	2	2	8	2		4	*	2	2	*			*		*
Gentiana corymbifera			t	t	2	t	1	t			1	2	t	1	*	t	*		*
Geranium microphyllum	2	1	t	*	*	*	t	*	*	*	*	*	*						
Geum parviflorum	1																		
Gnathalium traversii									*	*									
Haastia sinclairii						*							1	*				*	*
Hebe cheesemanii		t			*	t				t				*				*	*
H.epacridea		*		*		*		*		*			*					*	*
H.lycopodiodes	*	t	t	*	*	*	3	*	*	*	*			*					
H.odora			*			*													
H.pinguifolia	t	1	t	t	5	3	t	1	*	10			*	*				*	*
Helichrysum bellidioides										t									

Table 1 (cont.)

Plot	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	A3R	TR
Hieracium lachienlli		•																	
Hydrocotyle novae-zelandiae										•									
Leucogenes grandiceps		•				t		•		•			•	•			•	•	•
Lobelia roughii						•		•											
Meuhlenbeckia axillaris				•						3									
Myosotis spp																			•
Mysine nummularia			•	•	3		•												•
Notothlaspi spp		•				•		•											•
Oreomyrrhis colensoi	t								•										
Ourisia caespotosa	•	1	•	t				1		•	•	t	t						•
O.sessiliflora												t	•	•					
Phyllachne colensoi		•	t	t	2	•	2	3			1	t	1	2			•	•	•
Pimelea prostrata	•	t	1	•		t	2	•	•	•									
Pittosporum crassicaulae										t									
Pinus spp.							2	1											
Plantago novae-zealandiae	•	t	1	•						•	•	2	t						•
Podocarpus nivalis									•	•									
Pratia angulata	1	1	3	2	5	2	t	•	1	•	•	3	•	1	1	1	3	•	•
Pygmea pulvinaris													t					•	•
Ranunculus ensyii	•	1	1	•	•		t	2	t	2	•	•	•						
R.haastii		•		•				•											
R.insignis	t																		
R.sericiophyllus											t								
Rosulia bryoides						•												•	•
R.grandiflora			•	•	1	•	1	•			1	1	•	2	t	•	2	•	•
R.subsericea	•	t				3								•					•
R.hybrid spp.						t													•
Rumex acetosella	•	•	•	•	•	1	•	•	•	•									
Schizeilema Spp.	1	1								1	•	•							
Senecio lagopus	t	1	1	t	•	•	2	3	•	•	t	•	1	t				•	•
S.lyallii												•							
S.scorzoneroides			t		•					•	•	•							
Stellaria gracilenta			t						•	•									
S.roughii						1		•											

Table 1 (cont.)

Plot	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	A3R	TR
Taraxicum magellanicum	*	*			*		*		t	*	*					*			
Wahlembergia albomarginata	*	1	1	1	1	1	2	3	*	1	t	*	*	*	*	*	*	*	*
Viola cunninghamii	t	1	1	t	1	1	t	*	1		t	*	*	*			*		
LOWER PLANTS																			
Blechnum penna-marina	6	4	t	5			1		13	2	*	1	*						*
Hymenophyllum villosum							t												
Lycopodes australianum			*		t						t	1	*						
L.fastigiatum	4	1	5	2			1	1	*	*	1	*	t						*
Polystichum cystostegia	*	*		1					*	*	*	*	*	*			*		
Moss pavement	t	1	2	1	3	2	1	5	2	4	1	1	2	4	6	2	2	*	*
Lichen			t			1		1		t				*	*	*	*	*	*
OTHER CATEGORIES																			
Unidentified Litter	1	2	2		2	4	1	1	2	2	5	4	1	5	6	8	6		
Bare Soil	1	t	2	1	9	5	1	1	7	1	t	t	1	13	4	1	7		
Erosion pavement		12		5	3	20		6	1	6			22	7	1	13	26		
Scree pavement				15	1	3				21						21			
Rock				4	3	t	t			4	1	5	6	t	4	5	1		
Total Cover of Vegetation Alone (%)	134	125	129	114	127	114	125	123	119	125	125	130	117	115	110	107	117	-	-

NOTES:

t = Trace, represented in point analysis at < 1% of total hits

* = Presence observed in or near plots but not recorded from point analysis

** = Chionochloa pallens also included C.rigida and C.macra

However the number of plant species occurring in each plot varied from 24 to 63. The floristic list of species associated with each plot appears, in conjunction with the results of the quantitative analysis of vegetation, in Table I. The wide diversity in the taxonomic composition of plots was largely due to very minor species which frequently occurred with low constancy between plots.

Plot Description

In addition to the information summarised in Table I, information regarding the nature of cover in plots, its anticipated trend in condition under prevailing circumstances, and the nature of grasshopper populations occupying each site are pertinent to the study. These features are included below:

C1V Dense cover of Chionochloa pallens up to three feet high providing an almost closed canopy. Patches of Celmisia lyallii and open patches of Gaultheria depressa. Floor cover largely completed by Poa colensoi, Blechnum penna-marina, Lycopodes fastigiatum. Conditions under the dense vegetation moist. Early grasshopper instars were particularly associated with G.depressa patches. Watershed condition good, with trend anticipated as stationary.

C1S Vegetation similar to CiV but opening as it borders onto fine scree pavement. Celmisia lyallii more prominent

and with an increase in low growing species, e.g. Poa colensoi, Gaultheria depressa, Rumex acetosella, and Anisotome aromatica. Trend probably upwards.

C2V Tussock cover up to 2.5 feet high, much more open than C1V, but vegetation cover high. Subdominants of Celmisia lyallii, C.viscosa and C.spectabilis. Low cover of Anisotome aromatica, Drapetes dieffenbachii, Gaultheria depressa, Coprosma prumila and Lycopodes fastigiatum. The site is very favourable for Paprides and Sigaus australis, though because of good cover, trend is probably upwards under present conditions.

C2S Merges from C2V on to rocky scree. Celmisia lyallii dominant at expense of other prominent species in C2V.

C3S Remnant patch of vegetation bordered by coalescing scree. Protected from above by a bluff. Chionochloa pallens and Celmisia lyallii form codominants. Important minor species: Poa colensoi, Aciphylla monroi, Hebe pinguifolia and Dracophyllum pronum. The plot was steep, with much exposed soil, and indicating a downward trend in condition.

C4O Ridgetop site, very exposed to N.W. winds. Vegetation highly modified and open. Chionochloa rigida dominant, generally less than two feet high and windshorn. Species composition more in keeping with generally drier, more easterly locations. Intermediate cover provided by Festuca novae-zealandiae, Poa colensoi, Cyathodes and

Raoulia species. Trend downwards.

C5V Dense tussock cover up to three feet. S.W. aspect and moist. Intertussock cover is diffuse. Celmisia viscosa, Poa colensoi, Anisotome aromatica, celmisia lyallii, Dracophyllum pronum, Gaultheria depressa and Hebe lycopodioides prominent components. Experimental planting of pine trees, of Pinus mugo and P.contorta species are included in plots C5V and C5S. Trend stationary.

C5S More open than C5V, bordering sharply on to extensive scree area. Much cover of Dracophyllum pronum. Minor constituents: Poa colensoi, Anisotome aromatica and Cyathodes pumila. Trend stationary to upwards.

A1V Comparatively low altitude (4400 feet). Consists of dense Chionochloa pallens up to three feet high. Aciphylla squarrosa a prominent physiognomic codominant, but providing low total cover. Intertussock flora generally poor owing to density of Chionochloa. Celmisia lyallii, Blechnum penna-marina, and Poa mackayi important among minor components. Trend stationary.

A10 Open site on an outwash fan near A1V. Much intertussock space occupied by coarse scree. Shrubby plants common, reflecting scrub zone altitude, e.g. Hebe pinguifolia, Coprosma Cheesemanii, C.pseudo-cuneata, Gaultheria depressa and Meuhlenbeckia axillaris. Poa colensoi, Anisotome aromatica and Celmisia spectabilis also form

prominent ground cover. Trend dependent on extent of accumulation of material from above, though probably upward.

A2V The A2 location was on the lip of Alan's Basin and exposed to wind. Vegetation showing some windshearing. Tussock dense, up to two feet high where sheltered. Chionochloa pallens and Celmisia lyallii dominants, with Celmisia viscosa subdominant. Poa colensoi, Anisotome aromatica, Dracophyllum pronum and Drapetes dieffenbachii important components. Trend stationary.

A2V2 Snowgut site adjacent to A2V. Upper edge of hollow dominated by Chionochloa crassiuscula, and floor by Chionochloa oreophyla. This site was included because P.nitidus and S.australis congregated and fed on the open sheltered site in large numbers during favourable weather, though they moved back to more dense adjacent vegetation at night. Trend in cover stationary.

A2O Stabilised rocky scree and solifluction terrace area. Very exposed. Cover mainly of Dracophyllum mats. Sheltered hollows contained species of A2V. Trend variable, though probably upward, where stabilised by D.pronum.

A3S Remnant stand on the ridgetop at 6000 feet altitude. Surrounded by rock and scree. Celmisia lyallii dominant. Chionochloa up to one foot high. Dracophyllum pronum prominent on the periphery. Celmisia viscosa, Poa

colensoi, Notodanthonia settifolia form prominent ground cover, with Chionochloa oreophyla in an adjacent snow hollow.

A3R Very steep (43°) exposed rocky bluff occupied by S.villosus and B.nivalis grasshopper species. Scattered plants of Hebe cheesemanii and Dracophyllum pronum most common. Trend downward.

A4V Stabilised outwash fan. Somewhat open cover, much intertussock space covered by the moss Polytrichum juniperinum. Chionochloa crassiuscula a minor codominant with C.pallens. Celmisia lyallii subdominant. Poa colensoi and Aciphylla monroi are the only other important species. Floristically very poor (24 species). Trend upward.

A4O Adjacent to A2V. Not yet stabilised. Tussock being overwhelmed by debris from above. Decrease in Celmisia lyallii and Chionochloa crassiuscula compared with A4V, with Celmisia viscosa becoming prominent. Trend probably downward.

A5O Open site of sunny aspect. Erosion pavement occupies much of intertussock area. Other important ground cover provided by Notodanthania settifolia, Poa colensoi and to a lesser extent Anisotome aromatica and Pratia angulata. Trend in condition downward, though probably stabilising.

In addition to the plants mentioned above, some other species may occur with a generally high constancy rate in plots, though

they are of very minor importance in the cover they provide. Such species included Luzula rufa, Pratia angulata, Wahlembergia albomarginata and Viola cunninghamii.

Relative Grasshopper Numbers on Plots

It was revealed in the review of literature in Chapter 2, that the physical composition of grasshopper habitats, especially the height and density of vegetation, were an important factor limiting the distribution and abundance of grasshopper species. The following table affords some indication of the relative populations of grasshoppers on plots. No estimates were made of absolute populations. The estimates of grasshopper abundance were no more than observational comparisons gained from frequent inspection of plots, and from the collection of grasshopper specimens within. Estimates were classified into four classes of relative abundance as very low (VL), low (L), moderate (M), and high (H).

TABLE 2

Relative Abundance of Grasshoppers as Observed on Plots

	C1	VC1	SC2	VC2	SC3	SC4	OC5	VC5	SA1	VA1	OA2	VA2	V2A2	OA3	SA4	VA4	OA5	OA3	RTR
B.nivalis	-	L-M	-	M-H	L	M	-	M	L	M	-	-	M	H	-	M	L-M	L-M	L
P.nitidus	L-M	L-M	M-H	M	H	M	L-M	L-M	L	M	M-H	H	L	M	H	M	M	-	-
S. australis	L	L	M-H	M	H	M	L-M	L-M	L	M	M-H	H	L	M	H	M	M	-	-
S. villosus	-	-	-	-	VL	-	-	-	-	-	-	-	VL	L	-	-	-	H	L

Quantitative Analysis of Vegetation

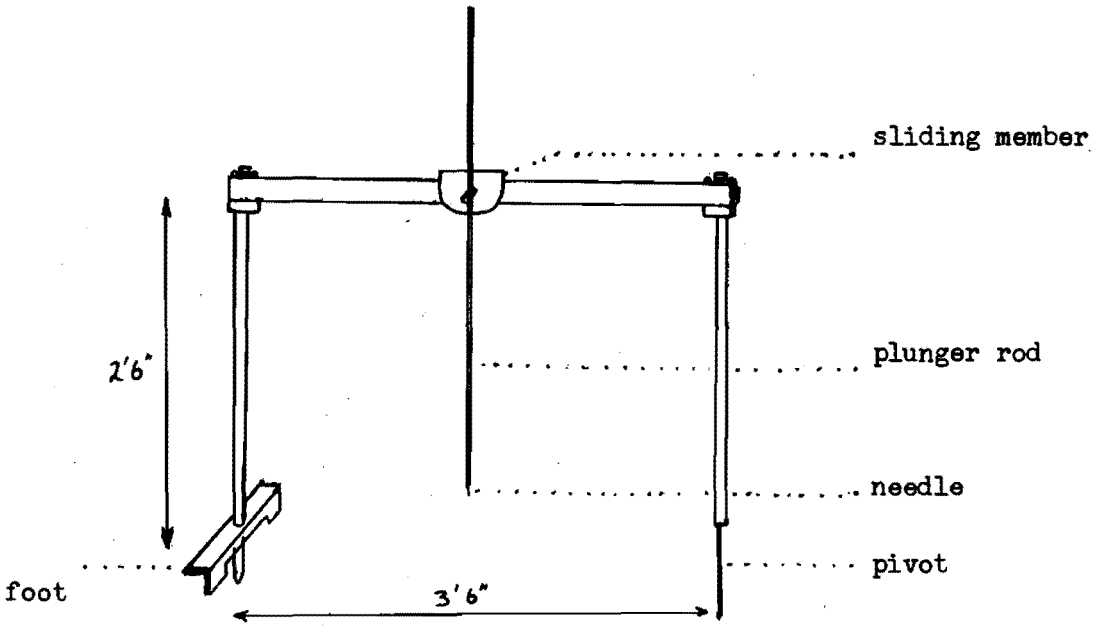
Equipment used in point analysis. The analysis of tussock vegetation by point analysis presented some problems not so readily encountered in lowland grassland vegetation (Scott, 1965). These are associated with the large difference in size between the tussock plants and the minor species, both of which required adequate analysis, and also with the slope of the terrain. The snow tussocks form the major cover, and physiognomic dominant, and to a large extent determine the microclimate within the vegetation. The canopy spread of these larger species vary at different levels in the vegetation, and the tussock basal diameter is very much larger than that encountered in lowland grassland situations. The minor species contributed in varying degrees to the floristic abundance of the vegetation, and consequently to the diet available to grasshoppers.

To help overcome the difficulties in measuring this type of vegetation, a modified point analyser frame was used. The frame was designed essentially to accommodate the height of the vegetation, and with point locations far enough apart to reduce the contagious effects on distribution, of measuring plant individuals of large basal diameter, whilst maintaining mobility. The frame, of collapsible aluminium alloy, consisted of two uprights fitting onto a connecting crossbar (Figure 2a). One of the uprights was extended to a point, to form a pivot when placed in the ground. The other had a foot

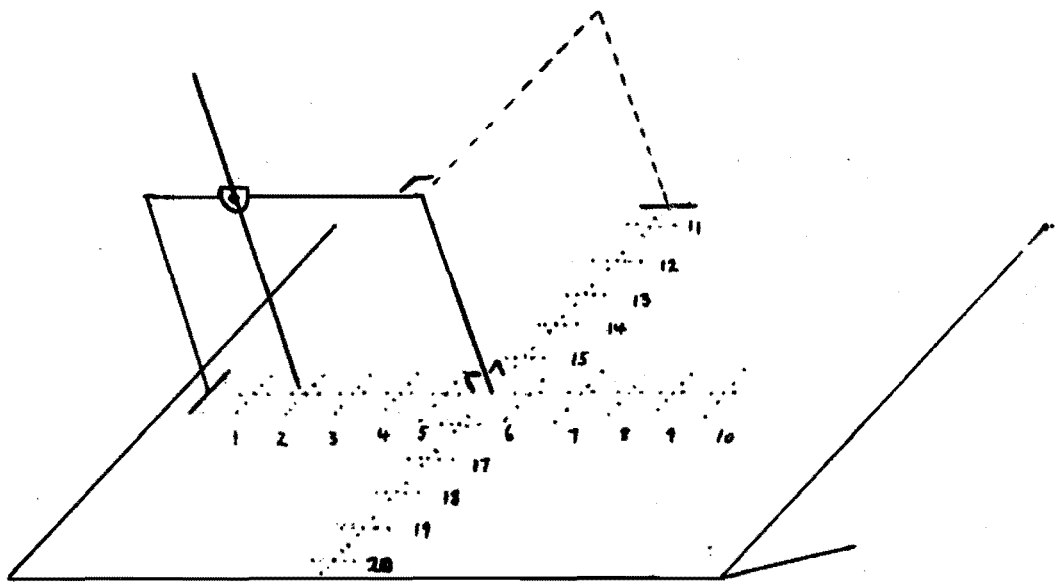
at right angles to the frame to enable it to lie in a vertical plane to that of the ground surface. By this means the point contact was projected towards the ground at as near constant angle as the terrain would allow (Fig.2, b). The point contact was provided by a needle fixed into the bottom of an aluminium plunger rod, which was in turn attached to a member on the crossbar by a spring loaded retainer through which it was allowed to slide. By sliding the crossbar member to fixed positions along the frame, five points were obtained at a spacing of about seven inches, for each placement of the frame. The needle had a vertical traverse over 2.75 feet.

One drawback with the frame was a degree of flexibility in the plunger rod resulting in some lateral movement of the pin point. Error in this respect was reduced by recording the vegetation contacted in a single downward stroke of the plunger. Radcliffe and Mountier (1964) found that when only contacts hit by the point of the needle were recorded, the area represented by the needle point, of less than .01 inches diameter, was negligible and could for practical purposes be considered as a true point.

Analysis of plot vegetation. The quantitative estimation of species composition was determined from 500 points, taken from 25 random locations located within the $\frac{1}{2}$ square chain area. The random positions were determined from a set of random numbers, paced out and pegged on a grid system, using a tape measure up one side of the plot as a guide. The analyser



a. The Point Analyser Frame



b. Method of Application of the Frame

FIGURE 2

Point Frame Apparatus used in the Analysis of Vegetation

frame was placed at each location using it as a point of pivot for the frame. Five readings were taken in each side of this point, across and with the slope, by rotating the frame on its pivot as indicated in Figure 2, b, giving a total of 20 points for each random location.

As the needle descended, the first contact with each plant species was recorded. Thus five hits on any species represented one percent of ground cover. Where plants were not contacted as the needle descended, then the alternative cover of litter or bare ground was recorded. Litter was identified in the case of major species, for which crown hits were also recorded separately. Mosses where contacted were not identified, except in the case of moss pavement consisting of Polytrichum juniperinum. The three species of Chionochloa pallens, C.rigida and C.macra were not distinguished, but were recorded as C.pallens.

Where no vegetation was hit, the exposed surface was recorded as bare soil, erosion pavement (stones $< \frac{1}{2}$ inch diameter), scree pavement (loose stones $> \frac{1}{2}$ inch in diameter), or bare rock (fixed stones).

The field analysis was carried out between late December and early February 1968/69. The time interval between the start and completion of the analysis ensured that plants were in similar phenological condition when analysed. The 1968 season was characterised by heavy snow which did not clear until November from some plots. However by the time of

analysis, most annuals and herbaceous perennials such as Gentiana corymbifera and Senecio scorzoneroides had achieved maximum basal area.

The results of the analysis appear in Table 1.

Presentation of Data

The raw data, expressed as a frequency, represents the relative proportion of each species in the vegetation and the ground cover occupied by them. Thus for a given species A

$$\% \text{ Cover (C)} = \frac{\text{total hits on A}}{500} \times 100$$

The cover frequency is therefore a description of the plot in quantitative terms and forms a good basis for comparing the composition and condition of plots, and for determining the relative value of components of the vegetation in conservation. Results of the vegetation analysis of plots, expressed as frequency in this form, are presented in Table I.

However only the vegetation component of plots was of interest to feeding grasshoppers. Because the vegetation occupied a variable total area in each plot, the absolute frequency does not truly represent, on a comparative basis between plots, what was available to the grasshopper, as food. Therefore plant species were expressed as the proportion of vegetation cover alone, in order to compare more directly the frequency of vegetation with that of ingestion by grasshoppers. Thus for the given species A,

$$\% \text{ vegetation cover (V)} = \frac{\text{total hits on A}}{\text{total points contacting vegetation}} \times 100$$

$$\text{or} = \frac{\text{total hits on A}}{500 - \text{points not striking vegetation}} \times 100$$

As an example, two plots both have 100 hits on species A, say Celmisia lyallii, but whereas in one plot all 500 hits contacted vegetation, in the other 100 of the hits occurred on scree. Thus for C.lyallii,

$$\% \text{ C in both cases} = \frac{100}{500} \times 100 = 20\%$$

$$\text{but \% V for the scree plot} = \frac{100}{400} \times 100 = 25\%$$

Thus a grasshopper searching for a feed on the open plot has a greater chance of contacting C.lyallii relative to other plants than on the plot with more extensive vegetation. Although absolute cover of Celmisia in each plot is the same, the relative frequency (or relative availability to grasshoppers) is not.

Further to this, upon analysing the vegetation each plunge of the needle might come into contact with more than one plant species in layered vegetation. The proportion of such multiple hits varied with the degree of layering of the vegetation in each plot. The number of different plant contacts per hundred strokes of the needle which contacted vegetation was found to vary between 114 and 130 (Table 1). Therefore to make the

plots completely comparable on the basis of availability of plants to grasshoppers, the vegetation cover (V) should be brought to base 100 by dividing by a vegetation factor, the number of species encountered per point contacting vegetation.

$$\text{Vegetation factor} = \frac{\text{sum total of species contacted}}{\text{total points contacting vegetation}}$$

$$= 1.1\text{-}1.3 \text{ in the present analysis}$$

Division of V by the vegetation factor then produces the relative frequency of a plant species within each plot. Thus for the species A

$$\%\ \text{Vegetation frequency (Vf)} = \frac{\frac{\text{total hits on A}}{\text{total points contacting vegetation}}}{\frac{\text{sum total of species contacted}}{\text{total points contacting vegetation}}} \times 100$$

$$= \frac{\text{total hits on A}}{\text{sum total of species hit}} \times 100$$

The significance of this ennunciation for comparing vegetation abundance with grasshopper ingestion is better appreciated when compared to that for grasshopper ingestion data on page 136 . The analysis of the vegetation, expressed as vegetation frequency, appears in conjunction with the grasshopper ingestion results in Table 7.

B. DETERMINATION OF GRASSHOPPER FEEDING HABITS AND DIET

Introduction

Familiarisation with the general behaviour and distribution of grasshopper species was achieved during the summer 1967/68. Populations of grasshoppers in alpine areas were investigated in the Craigieburn and Seaward Kaikoura Ranges, as well as those of lowland species, on Banks Peninsula and in North Canterbury.

In the subsequent season, field work for determination of the feeding habits of alpine grasshoppers was carried out at the Craigieburn site. Where possible observations of the general behaviour and selection of food were made when in the field. A further broad indication of feeding type was gained from investigation of the mandibular morphology. However epidermal analysis of grasshopper gut contents was the principal method used for diet determination in the present study. Because samples could be stored, this method enabled optimal use to be made of the short field season available, and also facilitated the accumulation of greatest quantity of data on feeding habits. The results related directly to the field conditions from which the grasshoppers were collected, and the form of data obtained could be related directly to the frequency of plant abundance obtained from vegetation analysis. Differential feeding tests were not attempted because the results so obtained would have borne little relation to the diet

selected under field conditions, where plant abundance is an important factor.

Because the feeding ranges of the four grasshopper species overlapped considerably, it was necessary to determine the food preferences of all species in order to gain some indication of the possible effects of grasshopper populations on the vegetation. Anderson and Wright (1952) and Mulker et al (1962, 1964), in finding wide differences in the feeding habits of different species, expressed the further need to consider each species separately.

The study was therefore pursued along the following lines:-

1. Preliminary work
2. Field observations of behaviour and feeding preferences
3. Estimation of food throughput in grasshoppers
4. Examination of mandibular morphology
5. Epidermal analysis of grasshopper gut contents

Preliminary Work

Attempts to assess grasshopper numbers during the summer 1967/68 revealed many difficulties that placed such an assessment beyond the scope of the present study. Major difficulties in the estimation of grasshopper populations, both

absolute and relative, were associated with the nature of cover, the topography, and the grasshoppers themselves.

(i) Vegetation and scree cover. The density, height, and lack of uniformity of vegetation, and the nature of scree surface varied greatly between and within sites. This afforded varying effectiveness of cover for grasshoppers which in turn affected differentially the efficiency of any method of grasshopper capture between sites.

(ii) Topography. When disturbed, the grasshoppers leaped at random. This resulted in a rapid movement downhill on steep slopes. Capture by hand or net was as a result, more difficult with an increasing degree of slope, and the displacement of the remaining grasshoppers due to the disturbance during capturing was greater.

(iii) Grasshoppers. Considerable differences existed in the relative ease of sighting and capture between grasshopper species, sexes and instars. Male S.australis were generally the most difficult to capture. These were well camouflaged on their ground surface background, and went to ground more readily than the others upon disturbance either by remaining inactive and unsighted, or by disappearing beneath vegetation. Adult female individuals were generally easiest to see and capture, being about twice the size of males, and less active or elusive. Grasshoppers that were away from their natural background were much more easily sighted than other species e.g. B.nivalis on vegetation.

Grasshopper activity varied greatly as influenced by time of day and climatic conditions. Maximum activity occurred in clear, calm and sunny conditions during early to mid-morning, and from mid-afternoon to sunset. Very little activity was evident before and after sunset, or when temperatures fell below about 45 - 50°F. In these circumstances the grasshoppers occupied sites in dense vegetation or beneath scree.

The following methods for estimating relative populations were given brief appraisal:-

(i) Time/capture counts

(ii) Systematic sweeping

(iii) Visual estimates (Batcheler, 1967)

(iv) Sticky traps using a non drying glue (No.437 adhesive manufactured by Davis Gelatine NZ Ltd.)

(v) Pitfall traps

Because of the great variability in conditions mentioned above it was difficult to obtain meaningful results, although some qualitative indication of relative population levels was gained from working with the grasshoppers.

The most promising method for rapid estimation of absolue populations appeared to be the night cage technique of Anderson and Wright (1952). A cage placed over the vegetation at night, when grasshoppers were inactive, retained grasshoppers which could be counted the following day.

A somewhat reliable technique for assessing overwintering

populations might be developed as a modification of the night cage method. Grasshoppers were observed to emerge in small enclaves of vegetation as soon as these became cleared of snow. The grasshopper population on the enclosed area could be estimated by capturing those confined to these patches. Those that jumped into surrounding snow during the capturing were very easily seen, soon became sluggish and were readily retrieved. By systematically clearing patches of snow from uniform areas of vegetation or scree, a systematic and accurate estimation of grasshopper populations could be obtained by these means.

Grasshoppers were recovered from several of these snow free areas in November 1968 in Camp Stream. Visitation to the areas on the day subsequent to the first removal of grasshoppers indicated that nearly all grasshoppers had been removed in the first sampling. It became apparent during this work that hatching of eggs occurred very soon after snowmelt had occurred and that the first instar was of short duration of a few days. The snowfree areas examined were pegged around the limits for later estimation of area and vegetation composition. Since the areas were small, they generally contained a limited and easily defined number of plant species from which the grasshoppers could select their diet. These grasshopper samples were therefore later used in the gut analysis work for initial familiarization with procedures and identification techniques. The results were not however included in the data

of grasshopper diet analysis. Dr. A.S.White (pers.comm.) is currently finding success with capture/recapture methods for the longer term study of the population dynamics and movements of the same grasshopper species as in the present study. Individual capturing of grasshoppers in plots, using a hand net is employed in the study.

Field Observation of Feeding Behaviour

Daily behavioural regimen. When in the field, observations, whenever possible, were made on the general behaviour of grasshoppers, both during the course of other work, and by specific observation of undisturbed grasshoppers.

In general, the daily behavioural regimen followed that of Chortoicetes terminifera, described by Clark (1947a). Between the hours of sunset and sunrise grasshoppers occupied shelter sites. In the case of the scree inhabiting species (B.nivalis and S.villosus), these sites were usually under coarse scree debris. They were observed to disappear generally by backing down into the inter-rock crevices. P.nitidus and S.australis roosted mainly in the bases of tall tussock plants. The common method of entry observed in P.nitidus individuals after alighting or climbing onto a tussock, was to back down a tiller as deep into the base of the tussock as possible, to remain in a vertical and upright position.

Grasshoppers which were followed to their sheltering positions in the evening were found to occupy the same position

the following morning prior to the commencement of activity, indicating that no nocturnal activity had occurred. Young instar grasshoppers of all species were seen to merely nestle under vegetation at or close to ground level and did not appear to be as reliant on either scree or tall dense vegetation as were adults.

Shortly after the rising sun had cast rays on the ground surface, the grasshoppers were seen to emerge from the shelter sites, and appeared in situations exposed to the direct rays of the sun. These were generally on open sites of low vegetation, rock, scree or soil cover in positions sheltered from wind. The grasshoppers oriented themselves to gain maximum exposure to the sun before settling down to bask. Prior to, and after feeding, preening and cleaning behaviour was frequently observed during which the front legs, either separately or in unison, were brushed over the top of the head and down the antennae.

Feeding behaviour commenced after varying periods of basking or warming in the sun and occurred throughout the day. However feeding activity was more pronounced between early and mid-morning and again during the late afternoon during hot sunny days. During feeding, the grasshoppers were observed to walk about with somewhat jerky movements and seemingly at random; or might take small jumps of a few inches prior to which they appeared to prejudge the landing site by scanning with antennae and eyes. On passing over objects, the surface

was actively surveyed with the antennae, labial and maxillary palpi. Indiscriminate biting also occurred frequently. On the larger broadleaved plants the grasshopper oriented itself by straddling the leaf margin before biting. If the plant was found to be acceptable, feeding ensued for varying periods, after which the grasshoppers may then have continued to feed on other leaves of the same plant, or another plant of the same or different species. A plant species rejected after a first nibbling may be fed upon after again being contacted. Feeding in this manner may last up to half an hour during which food from one to several plants may be consumed, while covering a radius of a few feet to several yards. After feeding, normal preening and basking again ensued.

The basking, done motionless in sheltered positions exposed to direct sunlight, may continue throughout the day in favourable conditions, though individuals generally did not remain long before moving to a new basking site or merely reorienting themselves. During hot weather grasshoppers moved to more shady sites near rocks or under vegetation during the middle part of the day. Much less frequently they were seen to climb onto tussock, apparently in order to expose themselves to the cooling effects of the breeze. Following a feeding period the grasshoppers moved to the denser shelter sites around sunset. This daily regimen was obviously in response to optional microclimatic conditions, particularly temperature. The diurnal shift to and from shelter sites appeared possibly to

occur as the differential temperature between the two sites coincided.

As well as the diurnal regulation of grasshopper activity, climatic conditions also had a considerable influence. Grasshoppers did not emerge at all during cold spells, and sought shelter during cool, cloudy or windy weather at any time of day. Activity appeared to be greatly reduced as atmospheric temperature fell below about 45 - 50°F.

Defecation by grasshoppers occurred throughout the day and might occur during or following feeding, apparently in response to fresh food displacing that of previous food in the gut. Frass was frequently flicked away from the abdomen by a rear foot. Sideways oscillation of the abdomen was sometimes observed during defecation presumably to assist the passage of food in the gut.

Grasshoppers were seen in copula at almost any time of the season. Males spent much time in the pursuit of females, whence the antennae were of conspicuous use in following her movements. The advances made by males were most usually rejected by the female jumping away. On occasions several males were observed in the pursuit and attempted mating of the same female. Males were also seen making approaches to females of different species, though never successfully, to the extent of actually mounting the female. Females when in copula appeared to carry out normal behaviour, though the males did not feed. Males very frequently emitted a sound which

appeared to emanate from scraping the mandibles together. Such a method of sound creation does not appear in the literature for other species of Acrididae. Stridulation does not appear to occur in these grasshoppers.

Egg laying occurred in warm sunny conditions, the few females that were observed usually excavating a hole with the abdomen on small erosion or bare soil patches among low vegetation. In many cases where ovipositал behaviour was observed, egglaying did not occur, for unknown reasons. As one particular instance, an ovipositing S.australis was observed at 4.00 p.m. on plot C5. It firstly attempted to lay in a Poa colensoi clump among Dracophyllum pronum. It later laid 42 eggs in erosion pavement under P.colensoi. Each egg, exuded with a white frothy substance, was emitted at 10 - 12 second intervals. The egg laying was concluded by leaping away from the site, which may have resulted from disturbance, and thence to normal sunbathing activity. Examination of the eggs several months after laying revealed that they had been parasitised with a Hymenopterous parasite of an unknown species.

Feeding selectivity. Because of the time required in watching an individual undisturbed grasshopper until it began feeding, records of plants selected by observed grasshoppers are few. Initially it was not appreciated the extent to which grasshoppers included several species of plants during a feeding period. The results of these observations are presented as individual grasshopper feeding records in Table 3. It

TABLE 3

Food Selected by Grasshoppers as determined from Direct Observations during the Study Period

Species			Age		Sex		Observation			Plant Species consumed (Plants nibbled only, in parenthesis)
Bn	Pn	Sa	A	J	M	F	Date	Time	Location	
x			x		x		7.11.67	10.00 a.m.	A 5	Celmisia laricifolia
	x		x			x	28.11.67	12.30 p.m.	A 1	Celmisia lyallii
x			x		x		"	"	"	Celmisia lyallii, Poa mackayi, (Prata angulata)
x			x			x	"	"	"	Poa colensoi
x			x			x	"	"	"	Poa colensoi
x			x			x	"	"	"	Blechnum penna-marina, Celmisia lyallii
x			x		x		"	2.30 p.m.	"	Chionochloa pallens
x			x			x	"	"	"	Poa colensoi
	x		x		x		"	"	"	Celmisia lyallii
	x			x		x	13. 2.68	9.00 a.m.	"	Wahlembergia albomarginata seedling (killed)
	x			x		x	"	"	"	Gnathalium traversii, Epilobium perplexum
x				x		x	"	"	"	Epilobium perplexum
	x			x		x	14. 2.68	8.30 a.m.	Ski Basin	Taraxicum magellanicum, grass species
	x		x			x	"	"	"	Anisotome aromatica flowerhead, Taraxicum magellanicum
	x		x			x	21. 2.68	9.00 a.m.	Kaikoura	Phormium colensoi
	x		x			x	"	"	Mountains	Coprosma cheesemanii
	x		x			x	"	"	"	"
	x		x		x		"	"	"	"
x			x		x		10. 1.69	10.00 a.m.	A 1	Pittosporum crassicaule
	x		x		x		"	3.15 p.m.	A 5	A.aromatica flower, Raoulia grandiflora
		x	x			x	"	4.00 p.m.	"	Pratia angulata (Polytrichum juniperinum)
	x		x			x	11.1 .69	7.00 a.m.	"	Polytrichum juniperinum, Notodanthonia
		x	x			x	"	"	"	settifolia, L.forsteri Lachnagrostis forsteri
	x		x		x		"	9.00 a.m.	"	Gentiana corymbifera
		x	x			x	"	3.30 a.m.	"	Celmisia lyallii
		x	x			x	"	"	"	(Celmisia viscosa)
x			x		x		12. 1.69	5.30 p.m.	A 3	Hebe pinguifolia flowerbuds
		x	x			x	"	6.00 p.m.	A 4	Aciphylla monroi flowerhead
	x		x		x		20. 1.69	5.00 p.m.	A 2	Chionochloa oreophyla
	x		x			x	"	"	"	Plantago novae-zelandiae
	x		x			x	"	"	"	Gentiana corymbifera
	x		x			x	"	"	"	Epilobium pedunculare, Anisotome aromatica
	x		x			x	"	"	"	Anisotome aromatica
		x	x			x	"	"	"	Drapetes deiffenbachii
		x	x			x	21. 1.69	8.00 a.m.	"	Anisotome aromatica
		x	x			x	11. 2.69	11.00 a.m.	C 4	Raoulia subsericea
		x	x			x	"	4.30 p.m.	C 5	Gaultheria depressa (Lycopodes fastigiatum)
	x		x			x	12. 2.69	1.30 p.m.	A 2	Celmisia dubia
	x		x			x	"	"	"	(Drapetes dieffenbachii)
	x		x			x	"	"	"	Rostkovia gracilis
	x		x			x	"	2.00 p.m.	"	Anisotome aromatica
		x	x			x	"	"	"	Plantago novae-zealandiae
		x	x			x	"	"	"	Senecio scorzoneroides, (Celmisia dubia)
		x	x			x	"	"	"	Ourisia sessilifolia
		x	x			x	"	"	"	Celmisia viscosa

Table 3 (cont.)

Species			Age		Sex		Observation			Plant Species consumed (Plants nibbled only, in parenthesis)
Bn	Pn	Sa	A	J	M	F	Date	Time	Location	
		x	x			x	12. 2.69	2.00 p.m.	A 2	Poa colensoi
	x		x			x	"	"	"	Chionochloa oreophyla, Celmisia sessiliflora (A.aromatica)
	x		x			x	"	2.30 p.m.	"	Rostkovia gracilis
x			x			x	"	"	"	Celmisia sessiliflora
		x	x			x	"	"	"	Anisotome aromatica
		x		x		x	"	3.00 p.m.	"	Chionochloa pallens seedling
		x		x		x	"	"	"	Rostkovia gracilis
		x		x		x	"	"	"	Celmisia viscosa
	x		x			x	"	"	"	Anisotome aromatica
	x		x			x	"	"	"	" " ,Chionochloa crassiuscula litter
	x		x			x	"	3.30 p.m.	"	Celmisia sessiliflora
	x		x			x	"	"	"	A.aromatica, C.sessiliflora
	x		x			x	"	"	"	A.aromatica
	x		x			x	"	"	"	Luzula rufa, L.rufa flowerhead
	x		x			x	"	4.00 p.m.	"	Chionochloa crassiuscula, A.aromatica
	x		x		x		"	"	"	Poa colensoi
	x		x		x		"	"	"	" "
	x		x			x	"	4.30 p.m.	"	Anisotome aromatica
	x		x			x	"	"	"	Poa colensoi (Polytrichum juniperinum)
		x	x			x	"	"	"	Anisotome aromatica
		x	x			x	"	5.30 p.m.	"	Forsera tennella
	x		x			x	"	"	"	Anisotome aromatica
x			x		x		"	"	"	Coprosma pumila (Dracophyllum pronum)
		x	x			x	"	"	"	Poa colensoi, Gaultheria depressa
x			x			x	1. 1.70	7.30 a.m.	A 2	Anisotome aromatica
x			x			x	"	8.30 a.m.	"	Celmisia viscosa
	x		x			x	"	"	"	Poa colensoi
	x		x		x		"	3.00 p.m.	A 3	Celmisia lyallii, Astelia nervosa
	x		x			x	"	5.30 p.m.	A 4	Poa colensoi
	x		x			x	"	6.00 p.m.	A 4	Gentiana corymbifera (Raoulia grandiflora)
	x		x			x	"	"	"	G.corymbifera,P.colensoi,A.aromatica (C.oreophyla,D.pronum,C.lyallii)
	x		x			x	2. 1.70	6.30 a.m.	"	C.viscosa,A.aromatica,Lachnagrostis forsteri seedhead
		x	x			x	"	"	"	A.aromatica flowerhead,P.angulata, (R.grandiflora)
		x	x			x	"	7.00 a.m.	"	Anisotome aromatica, Polytrichum juniperinum
		x	x			x	"	7.30 a.m.	"	Poa colensoi

Note : Bn = Brachaspis nivalis
Pn = Paprides nitidus
Sa = Sigaus australis

A = Adult
J = Juvenile
M = Male
F = Female

Chionochloa pallens includes C.rigida and C.macra

became apparent from this aspect of the study that grasshoppers of all species exhibited rather general habits, and consumed not only a wide range of grasses and forbs, but also moss and fern species. No marked trends were evident in the type of food selected, or of differences in selectivity between species. It is of interest also that a wide range of non-green vegetable matter was also consumed. Several were observed to feed upon dried litter material of grass and forb origin and also upon Hare faeces. One was observed to feed on a woollen shirt left on the ground. Subsequent analysis showed its crop to be full of wool. Another individual drew blood in its undisturbed attempts to feed on the back of a human hand resting on the ground, and a further two individuals from the gut analysis contained considerable quantities of plastic, probably originating from a plastic bag ! Quite large numbers were observed from gut analysis to contain insect fragments in sufficient quantities to indicate that their occurrence did not arise from accidental consumption.

Evidence of grasshopper feeding damage. In order that the feeding damage of grasshoppers might be distinguished from that of other phytophagous insects, grasshopper feeding was observed in respect of the type of damage inflicted. Grasshoppers were observed to be principally feeders on the margins of the leaf lamina, in the manner described by Gangwere (1965a) and Williams (1954). However, damage caused by grasshoppers in the present study was evidenced in a number of

forms which depended largely on the growth form and leaf type of plant species, but also on the mode of feeding adopted by the grasshopper. Types of feeding may be categorised into the following classes on the basis of damage apparent:

(i) nibble. This was evidenced by a small nip on the leaf margin, or a bruising of tissue as a result of test biting and subsequent rejection of the leaf by the grasshopper.

(ii) scallop. This feeding was the typical damage resulting from normal feeding on the leaf margin of larger leaves e.g. on Celmisia viscosa, Gentiana corymbifera and Chionochloa pallens. It appeared as a concave area of leaf removed from the margin. Feeding of this type may penetrate to the midrib or sever the leaf entirely. In this feeding the grasshopper straddled the leaf margin and consumed food in downward swathes of the mandibles. Similar damage was also caused by weevils, especially on C.lyallii, though this was generally distinguishable by its less symmetrical concavity.

(iii) emargination. In this type of damage, feeding commenced in the normal manner, but the margin of the leaf separated from the remaining leaf with the first incision. The grasshoppers continued to feed down the strip of leaf, resulting in the loss of a thin strip along the leaf margin. This damage was especially evidenced on broad leaved grasses and Celmisia lyallii.

(iv) midrib feeding. Where leaves occurred in

folded form, or with a very prominent midrib, the grasshopper straddled the centre of the leaf to produce damage as a bisymmetrical window in the open leaf. Such damage was particularly evident on Chionochloa crassiuscula.

(v) leaf tip feeding. In the case of very narrow leafed plants e.g. Celmisia laricifolia, Poa colensoi, and Dracophyllum pronum, the grasshopper was observed either to commence feeding on the tip of the leaf and continue feeding down the axis of the leaf, or the leaf was severed near the base, and the severed section fed into the mouth while held between the front legs. This type of feeding may also occur with finer flowering stems e.g. that of Anisotome aromatica.

(vi) consumption of entire leaves. Where leaves were small or uneven in outline the entire leaf was consumed, usually leaving only the pedicel remaining on the plant. This occurred in species such as Coprosma species, Anisotome aromatica and Pratia angulata.

(vii) bud nipping. Bud nipping was especially prevalent on shrubby species e.g. Hebe pinguifolia, Coprosma pseudocuneata and Drapetes dieffenbachii. The flower or leaf buds were eaten or damaged either by feeding from the sides of the larger buds, or from eating down into the bud from the top. Such feeding often resulted in death of the stem and eventual "dieback" in the plant if severe.

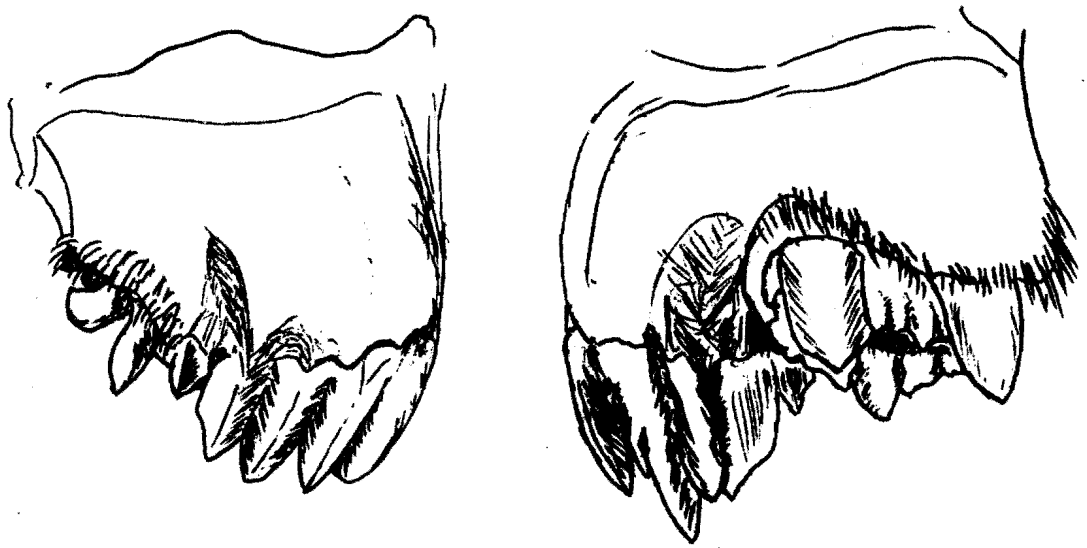
(viii) barking. Grasshoppers also caused damage to new shoots of shrubby plants by bark biting which resulted in

death of young growth from ringbarking in extreme cases.

(ix) surface feeding. This damage to the surface of leaves largely occurred from the feeding of younger instars on the smooth surface of hairy leaves e.g. Celmisia spectabilis, C.lyallii, or where leaves were otherwise too thick margined to be embraced by grasshopper mandibles e.g. Hebe pinguifolia.

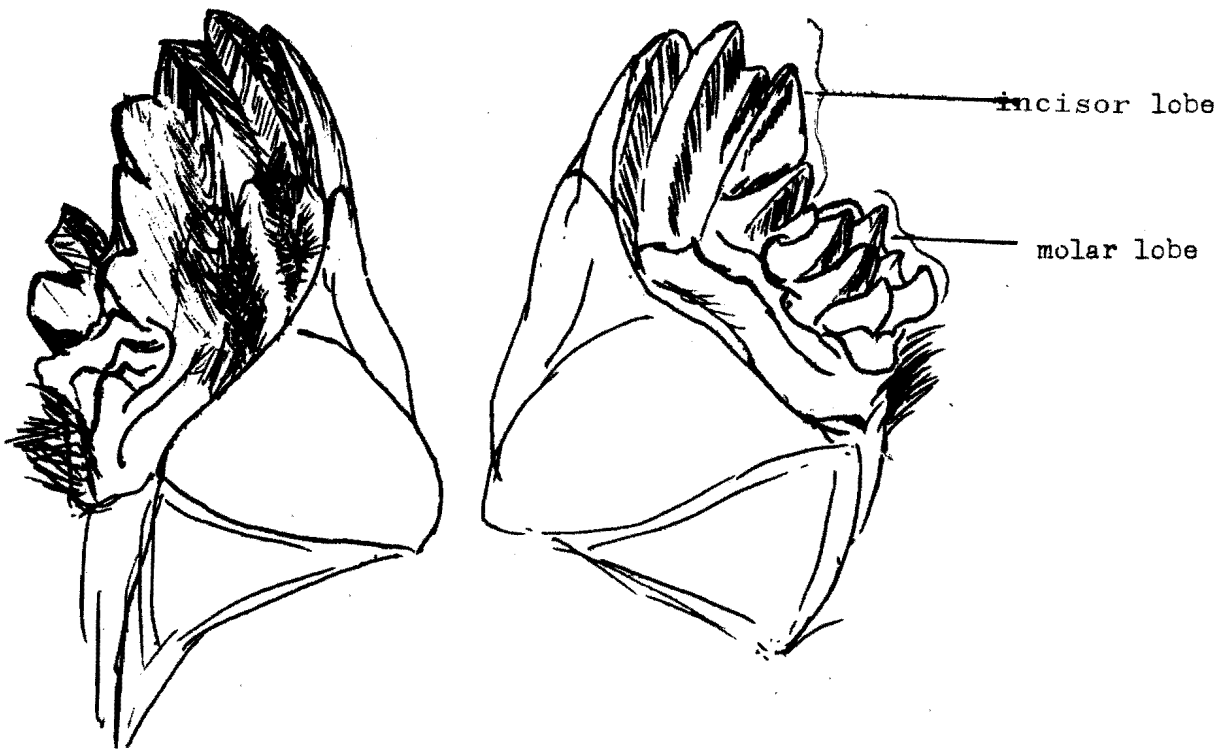
Examination of Mandibular Surfaces

As a preliminary to gut analysis some indication of the general feeding type of grasshoppers, as revealed by the mandibular biting surfaces was obtained. The heads of recently moulted male and female adults of the four species were obtained so that the mandibular surfaces would be fully developed in the absence of wear. Mandibles were mounted on slides in glue to obtain dorsal, mesal and ventral views of the biting surfaces. The typical mandibular configuration is represented in Figure 3 and compared with mouthparts of Locusta migratoria, a typical grassfeeding type. The four species were all found to be of the forbivorous character described by Isley (1944) and Gangwere (1965b). This contrasted little with the mouthpart type expected for grasshoppers of the Catantopinae Subfamily, which are of characteristically mixed feeding habits, with a preference for forbs.



Left dorsal

Right dorsal

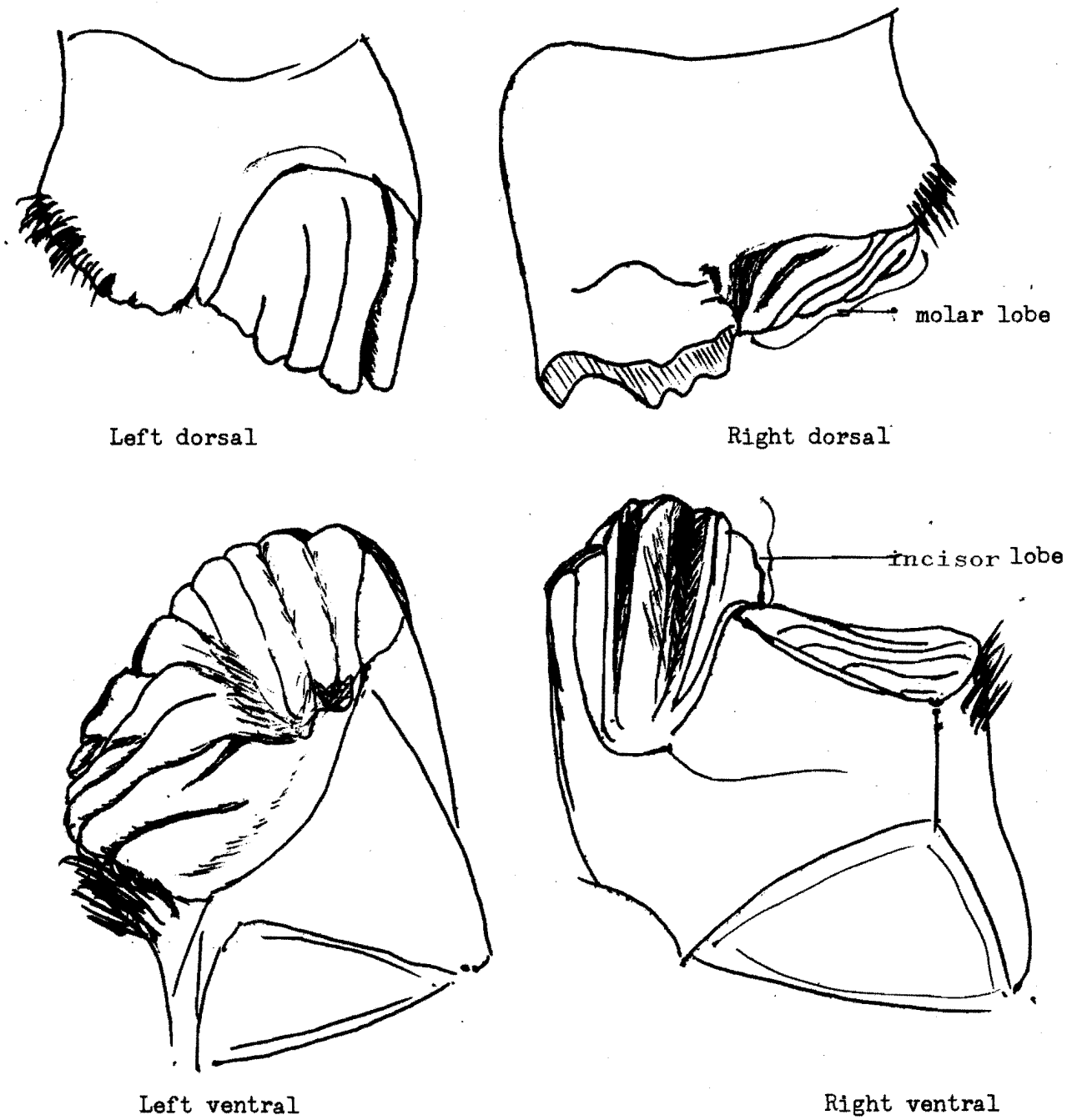


Left ventral

Right ventral

FIGURE 3

Configuration of Mandibular Surfaces of
Craigieburn Grasshopper Species showing Forbivorous Adaptations.



Left dorsal

Right dorsal

Left ventral

Right ventral

FIGURE 3 (contd)

Mandibular Surfaces of Locusta migratoria L.
to show Typical Graminivorous adaptations.

Throughput of Food in Grasshoppers

Since grasshopper feeding was observed to take place predominantly in two periods of the day it was of interest to determine the likely origin of food in different sections of the digestive tract at the time of sampling. It was desirable to determine whether or not the contents of the crop and hind gut represented different feeding times, and whether the hind gut samples were comparable with crop contents. If so, the grasshopper sample could be effectively doubled by analysing both the crop and hind-gut. It was observed that the fragments from the hind-gut were fully recognisable.

To answer these questions laboratory and field observations were conducted.

Laboratory test. The overall sparseness of the grasshopper population, and the difficulty of capture and maintenance of sufficient numbers for the laboratory, mitigate at present against extensive laboratory experimentation. However 45 adult male grasshoppers (by reason of convenience of size) of P.nitidus and S.australis were collected from a snow hollow site at 9.00 a.m. on January 3rd 1969. They were retained in containers with Chionochloa oreophyla vegetation, which was the dominant species on the collection site, until they were removed into three cages at Lincoln on January 4th at 3.00 p.m. The grasshoppers had access to water only, until the cages were treated separately the following day thus:-

Cage 1. This was placed on ryegrass/white clover

pasture at 8.00 a.m. on January 5th, whence feeding began immediately. The grasshoppers were removed from the pasture after one hour and given water only. Two grasshoppers were removed at intervals prior to and after the commencement of feeding and preserved in glycerine alcohol for later gut analysis. Of those remaining in the cage, the frass deposited was counted and removed for analysis at similar intervals.

Cage 2. This was also placed on the pasture at 8.00 a.m. with Cage 1, but remained on pasture until sundown at 6.00 p.m., the normal time for grasshopper activity to cease. Again two grasshoppers were removed at intervals, and frass counted as for Cage 1.

Cage 3. This was placed on pasture at 5 p.m. on 5th January, coinciding with late afternoon feeding times, and removed after one hour and again treated as for Cage 1. The temperature recorded throughout the experiment, did not fall below 65°F, which was well above the level for normal activity, both day and night. All species were previously observed to readily accept lowland plant species as food, and in fact showed that most common pasture grass and broadleafed species were highly favoured.

The characteristics of feeding and passage of food in the gut was evidenced by fragment counts of the crop, hind-gut and frass. The dimensions of grass and clover fragments were observed to be roughly similar. Since the grasshoppers used in the experiment were of one class (adult males) the fragment

TABLE 4

Experimental Observation of Food Throughput in Adult Male S.australis and P.nitidus

(by successive killing, and assessment of gut content and frass production)

	CAGE 1							CAGE 2							CAGE 3						
Date	1	2	3	Crop 4	5	Hindgut 4	5	6	7	1	2	3	Crop 4	5	Hindgut 4	5	6	7	1	2	3	Crop 4	5	Hindgut 4	5	6	7
Jan.5	8.00 am	-	Sa Sa	no trace "	" "	no trace "	" "	-	17	8.00 am	-	Sa Pn	no trace "	" "	no trace "	" "	-	15	5.00 pm	-	Sa Pn	no trace "	" "	no trace "	" "	-	13
"	9.15 am	1¼	Sa Pn Pn	56 249 87	57 1 190 full, tight	26 8 4	- - - filling	-	15	6.00 pm	-	Sa Pn	- 182 70	85 full, tight	81 44	24 3 full	-	13	6.00 pm	1	Sa Pn	111 83	92 200 full, tight	3 11	- filling	-	11
"	9.45 am	1¾	Sa Sa	19 47	149 283 full	19 11	31 41 full	4	12	8.30 pm	1½	Sa Pn	209 68	13 34 full	49 15	8 4 full	25	11	6.30 pm	1½	Sa Pn	157 165	96 25 full	17 4	13 2 full	1	9
"	10.15 am	2¼	Sa Sa	- 84	181 99 full	2 28	2 - defe-cated	7	10										7.30 pm	2½	Pn Pn	197 54	- 107 full	15 27	56 3 full	3	7
"	11.15 am	3¼	Sa Sa	- 9	93 91 flaccid	27 5	24 25 full	16	8										8.30 pm	3½	Sa Pn	147 260	- - full	58 85	- - full	2	5
"	1.15 pm	5¼	Sa Pn	62 -	- 10 ½-near empty	50 -	- 23 full	15	6																		
"	5.15 pm	9¼	Sa Pn	- -	- - empty	2 9	10 - near empty	20	4																		
"	7.30 pm	11½	Sa Pn	no trace "	" "	no trace "	" "	2	2																		
Jan.6										7.30 am	13½	Sa Pn	1 78	14 - ½-near empty	13 30	20 - full	48	9	7.30 am	14½	Pn Pn	17 114	109 17 flaccid	20 43	29 full	16	3
"										10.00 am	16	Sa Pn Pn	no trace " "	" "	no trace "	" "	9	7	10.00 am	17	Pn	no trace		no trace		-	1

KEY:
1. Time of day
2. Time elapsed from commencement of grasshoppers feeding
3. Species killed at time (1) Sa = Sigaus australis Pn = Paprides nitidus
4. Number of grass fragments
5. Number of clover fragments
6. Number of frass pellets removed at time column 1
7. Number of grasshoppers remaining during previous time interval to time in 1.

counts for each individual were assumed to be comparable to that of the other grasshoppers. Results are presented in Table 4.

Bearing in mind the limitations of the experiment with regard to numbers of grasshoppers used, the following observations were made:-

(1) Feeding began soon after placement of grasshoppers on the pasture, eating continued until the crop was full, within an hour from commencement of feeding. (Cages 1 and 3). The grasshopper guts were empty at time of placement on the food.

(2) Fragments began to appear in the empty hind-gut within an hour from commencement of feeding. (Cages 1 and 3).

(3) The hind-gut became full after two hours, with the formation of frass pellets in the hind-gut. Defecation occurred soon after two hours from the commencement of feeding after the morning feed (Cage 1). (The first frass appeared after $1\frac{1}{2}$ hours, consisting mainly of metabolic waste material and little plant matter.) The movement of food in the morning fed grasshoppers continued throughout the day, with crops appearing near empty after five hours, and empty after nine hours. The hind-gut became empty sometime after nine hours.

(4) There seems to be greatly reduced throughput of food at night in grasshoppers, even though the temperature

remained high. Guts became empty soon after daytime activity recommenced (Cage 2 and 3). This lends support to the field observation that there is very little activity of grasshoppers during nighttime hours.

(5) There was no preference shown for either grass or clover species, and no observable difference in feeding habits of the two species of grasshopper.

(6) The hind-gut was observed to contain a maximum of two formed frass pellets at a time, whereas the crop contents consisted (by fragment counts) of the equivalent of 6 - 10 pellets. Therefore the contents of the hind-gut as analysed for epidermal analysis was not fully representative of the contents of the crop.

(7) The number of fragments per pellet varied with the feeding time, being highest in the grasshoppers that fed throughout the day. This possibly reflected the better mastication of food consumed once hunger had been overcome. An average of 220 and 180 fragments contained per grasshopper estimated in cages one and three respectively, contrasted with 360 fragments per grasshopper from grasshoppers in which the entire digestive tract had become full (Cage 2), indicating that the fully satiated grasshopper contains approximately one and a half to two times that obtained from a single feeding.

Field observations. Several grasshoppers were observed in what they consumed while feeding in the late afternoon before disappearing into dense vegetation. They were then

traced to their places of overnight rest in tussocks, and were subsequently recovered from these places the following morning at sunrise. The guts were later examined in the laboratory. The crops were found still to be reasonably full, and to contain fragments of plants upon which they had fed the previous night. The hind-gut contained fragments of plants in addition to those species which grasshoppers had been seen to consume, indicating that the hind-gut contained the remains of a previous feed. The climatic conditions at the time the observations were made were highly favourable to optimal grasshopper activity.

The observations made during this test indicated that there was no movement of a taxic nature at nighttime, and that further to this, there was also very little metabolic activity with respect to movement of food through the gut. Defecation was seen to occur soon after the commencement of activity and feeding in the morning, and to continue throughout the day. This pattern of the continuous movement of food during the day, and restricted movement at night complemented that observed for the grasshoppers in the laboratory experiment.

Conclusions. It was concluded from these experiments that the contents of fore and hind-gut sections of the alimentary tract did not necessarily represent the menu from separate meals. However by analysing the hind-gut contents as well as those of the crop, a more comprehensive coverage of the overall intake of plant species by grasshopper individuals could be obtained. Hind-gut contents were also not comparable

with the crop which at capacity contained several times as many food fragments.

Analysis of both crop and hind-gut contents were subsequently used in the main analysis of grasshopper diet. The contents of each were recorded individually, but pooled as one sample in the analysis of results.

Epidermal Analysis of Grasshopper Gut Contents

Introduction. This formed the main basis for the determination of the diet, and food preferences of the four grasshopper species. The work involved could be divided into four main phases as follows:

(i) collection of plant specimens
(ii) preparation of a reference collection of leaf epidermis specimens
(iii) collection of grasshopper specimens
(iv) analysis of gut contents

As stated previous, much of the field work, including the collection of plant and grasshopper specimens was completed during the 1968/69 summer. A further limited grasshopper collection was taken in the summer 1969/70, largely to compare the intake of flower parts by grasshoppers during the prolific flowering season of 1968/69 and that of the less prolific season following it.

Collection of plant specimens. The study required the collection and identification of all plant species likely to

have been contacted in each plot by the grasshopper sample. A representative collection of all plant species encountered in or near the sampled plots was made, and stored in tubes of botanical FAA solution (85 parts 70% ethanol, 10 parts 40% formaldehyde and 5 parts glaceal acetic acid). This was in addition to the assessment of vegetation in plots as described under the analysis of vegetation.

It was noted from earlier feeding observations and from field damage that grasshopper feeding occurred principally on the leaf lamina. Gut analysis was subsequently aimed at the determination of leaf fragments only. The seasonal importance of flowers in the diet was underestimated as later revealed by gut analysis. However by similar comparative examination of morphological characteristics it would also be possible to identify these structures to species. Mosses and lichens were also recorded, but not identified.

Preparation of an epidermal reference collection. The preparation of a reference collection of epidermal specimens involved the separation of the cuticle and associated epidermal cells from the remaining leaf tissue, and subsequent clearing, staining and mounting of the specimens to obtain a surface view of the leaf epidermis of each species. To facilitate the identification of unknown leaf fragments, a keying system was then constructed from the reference slides.

(i) Preparation of cuticles before staining. Mulkern et al (1962, 1964, 1969) have conducted the only

comprehensive studies on grasshopper diet using the cuticle analysis technique. For these studies, type reference slides were prepared from fragments after various parts of the plant had been beaten in a Wareing Blender. Where this method was not found satisfactory, particularly with grasses, the cuticles were scraped clear with a razor blade and water, with KOH sometimes being used as a softener. (Mulkern and Anderson, 1959).

In the present study the aim was to mount as much of each surface of a leaf as possible intact. Slides were therefore prepared in a manner which enabled the ready comparison of both upper and lower surfaces, and also features of the leaf margin, costal, intercostal and midrib areas where possible, all mounted on one microscope slide. Thus the individual features on these leaf parts, the combination of which contribute to the identification of fragments, were all present in close and natural proximity.

The leaves were prepared in slightly different ways prior to the separation of the epidermis from the mesophyll tissue, depending on the size and shape of leaf as follows:

(a) Very small leaves and leaflets of compound leaves. These were either bisected by passing a razor blade between the upper and lower surfaces when pressed between microscope slides e.g. Coprosma species; or the leaf margin was cut around the leaf, leaving one straight margin intact e.g. Anisotone aromatica. In the latter case, when the

mesophyll was softened the two leaf surfaces were opened like a book to give adjacent exposure of the two surfaces separated by the leaf margin area.

(b) Larger leaves of forbs and grasses e.g. Celmisia and Chionochloa species. These were prepared from a section of leaf midway along the leaf lamina. A section of about ¼ inch long was removed and preferably extending to just beyond the midrib into the leaf. Again when the mesophyll was softened both surfaces were exposed, with leaf margin area in between. With densely tomentose surfaces of leaves e.g. Celmisia and Raoulia species, preparations with the tomentum intact and removed, were prepared.

(c) Very narrow elongate leaves such as those of forbs e.g. Celmisia laricifolia and grasses e.g. Poa colensoi. These were prepared from entire sections of leaf from midway along the lamina, with a longtitudinal cut made along the epidermis (preferably down the leaf margin) to facilitate opening of the two surfaces after the softening treatment.

Clearing of the epidermis from mesophyll tissue was largely achieved using the acid treatment of Croker (1959). The prepared leaf sections of each species were warmed in dilute HNO_3. The acid was usually about 70% strength but depending on the toughness of individual leaf tissues. Warming continued at below boiling until hydrolysis of the mesophyll tissue had been completed, evidenced by a cessation of bubbling from the leaves. Too strong acid or heating resulted

in the epidermis breaking away from the cuticle, and eventual destruction of the cuticle, while with insufficient acid treatment the mesophyll could not be separated from epidermal cells.

After warming in acid, the specimens were transferred to water made alkaline with ammonia, and subsequently handled by camelhair brushes. The sections were placed on slides, and where applicable, the surfaces were separated by folding the uppermost one back using needles. The softened mesophyll tissue was then removed by camelhair brush to expose the epidermal cells attached to the cuticle. The specimens were washed by irrigation with 30% alcohol prior to staining.

A few cuticles were too delicate to withstand acid treatment e.g. Geum and Acaena species. It was found that after soaking these specimens in commercial bleach for about five hours instead of heating in acid, they could then be handled as for other cuticles.

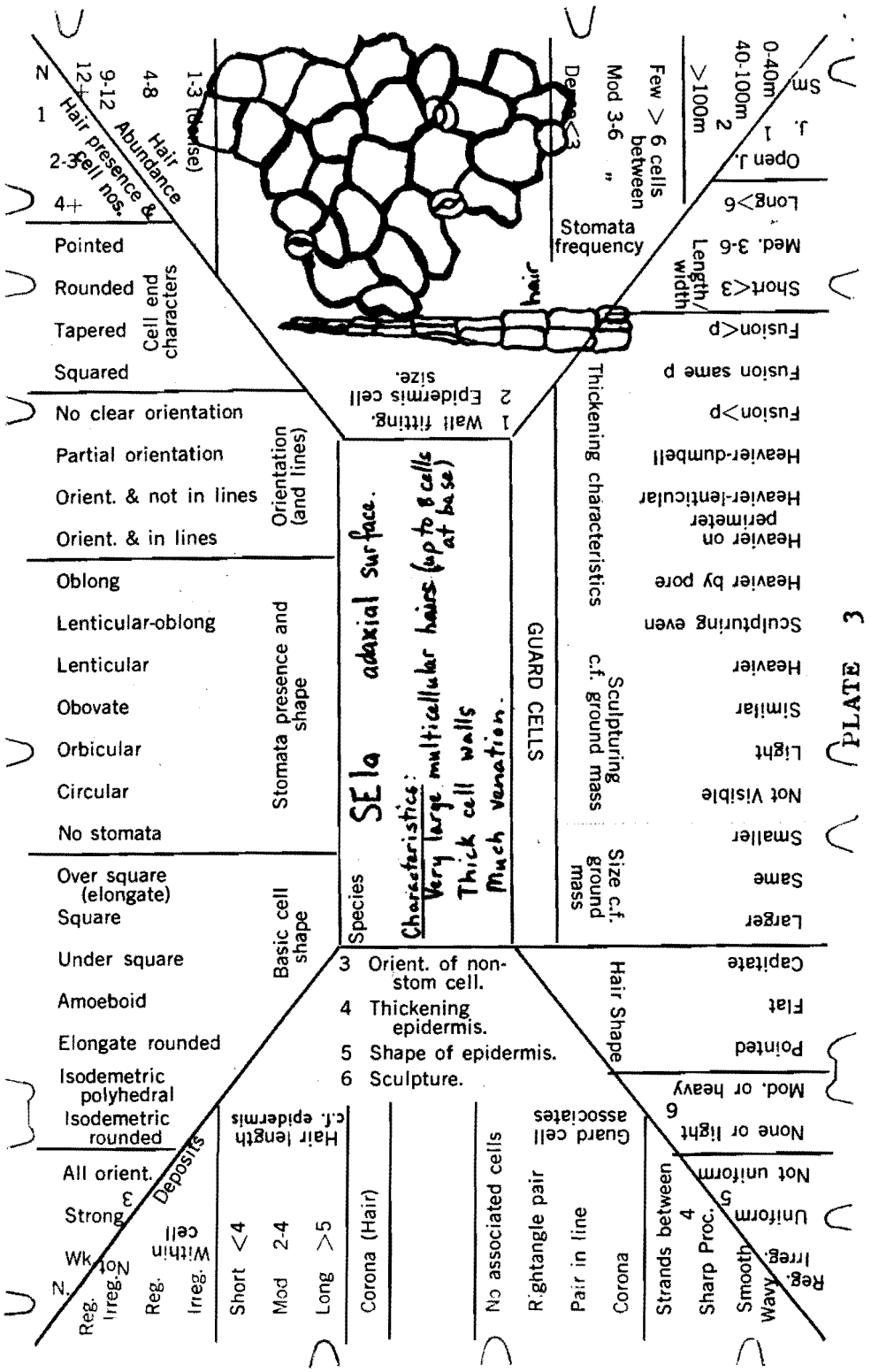
The larger clear epidermal specimens of both abaxial and adaxial surfaces were then ready for staining and mounting procedures.

(ii) Staining and mounting. Staining lent contrast to the clear transparent cuticle specimen, permitting better differentiation between structures of both the cuticle and underlying epidermal cells. Many stains have been used by the various workers. Of these, staining with 10% carbol fuchsin (C.L. Batcheler, pers.comm.) proved to be the most

effective and convenient. After irrigation with 30% ethanol, a drop of 10% carbol fuchsin was placed over the cuticle section on the slide. This was left for five minutes before again being washed in the alcohol solution and removal through a 30, 50, 90, 95 and 100% alcohol series. Initially the cuticles were mounted on an albumen smeared slide and dried prior to staining. However it was found best not to let the cuticle become dry at any stage, and to mount the cuticles after transferring them through the alcohol series by brush. Cleaning in xylol was not found to be necessary before mounting. After removal from the absolute alcohol, the cuticles were mounted face up. The cuticle was spread out with a brush constantly moistened with absolute alcohol, before placing a drop of enparol mountant and cover slide over the specimen. The slides were then dried in an oven for at least three days at 40°C.

(iii) Keying. Various keying systems may be utilized for identifying cuticles. Mulkern et al (1962, 1964) used a couplet system devised by Brusven and Mulkern (1960). However, in constructing their key, Brusven and Mulkern (1960) experienced some difficulty in separating all species into individual couplets. Such keys are frequently supplemented by the use of photographs and diagrams.

In the present study use was made of a punched card index system devised by C.L. Batcheler (pers.comm.) and featured in Plate 3. Although developed for classifying



Example of Punch Index Card used in Keying of Leaf Epidermal Reference Collection
(Example is of Senecio lagopus)
(developed by C.L. Batcheler, pers.comm.)

cuticle rather than epidermal specimens, this system was found to be very convenient to use and adequate for the present study. The advantage in using a card index system was the facility for recording and being able to utilise the whole combination of features which help to identify the cuticle. A photographic collection was not found to be necessary, although diagrams of general cell shape and unusual features made on the index cards were found to be beneficial. Use of the cards enabled elimination of all but a few species when identifying gut contents. Reference to the vegetation present on the grasshopper collection site further reduced confusion by elimination. If confusion still prevailed reference was made directly to the reference slides, thence to a comparison of freshly macerated leaves prepared from the preserved plant specimens mounted on slides and cleared in bleach.

Later identification of gut contents became largely a matter of familiarity and the rapidity with which each specimen could be analysed greatly increased.

Collection and storage of grasshopper specimens.

Grasshoppers were collected from the plot sites in three major periods during the summer 1968/69 principally so that seasonal chan ges in diet might be revealed. The collctions were made in early December, late January and March. After the extent of flower consumption in the later samples became apparent, a further collection was carreid out on some plots in January

1970, to compare the difference in flower intake between an abundant flowering season and that of the poorer season following. This sample was made to coincide with the late January sample of the previous season, when flowers were most abundantly represented in the grasshoppers.

Collections were made only during favourable climatic conditions to ensure maximum grasshopper activity and adequately full crops. Sampling commenced in the morning after opportunity had been given the grasshoppers for undisturbed feeding. This was generally one or two hours after the sun bathing the ground. As noted by Mulkern et al (1962) grasshoppers collected in the early morning after cold rainy or windy conditions the previous day, contributed to a high occurrence of empty or near empty crops. The grasshoppers were captured in the vicinity of the plots in which the vegetation analysis was conducted, and within an area over which the plot was considered to be representative. Observations had indicated that movement of grasshoppers in undisturbed conditions was limited to the extent that it could reasonably be assumed that they had fed within the capture area.

Because of the overall sparsity of the grasshopper population, grasshoppers were captured individually by hand, or with the aid of a net. They were caught as encountered by systematically covering the sampling area. This method resulted in least disturbance to grasshoppers, which disappeared under cover if disturbed indiscriminately, or moved

out of the plot area. The method also enabled the best representation of the overall plot population that was possible. Although all grasshoppers were collected randomly where possible, emphasis was given throughout the study to adults which, on the basis of observations of Putnam (1963) and Bullen (1966), were assumed to be causing the greatest amount of total damage.

Grasshoppers were put into collection tubes of 70% glycerine alcohol by species, in which they were stored until subsequently removed for gut analysis. Sampling in each plot usually proceeded until one tube became full (about twenty adults) or until grasshoppers became too scarce (generally after about one hour of searching).

Analysis of gut contents. As a result of feeding trials it was decided to analyse both the crop and hind-gut contents of adult grasshoppers. Only the crop was analysed in other instars. The grasshoppers, removed from the glycerine alcohol storage in the laboratory, were decapitated in a manner that the crop remained attached to the head and was pulled clear of the body, with the head. Similarly the hind-gut, usually containing one or two frass pellets, was withdrawn with the hindmost segments of the abdomen. The gut sections were placed on separate microscope slides, split open with pins, and the contents removed onto the slide. These usually rolled free of the gut wall as a bollus. A few drops of diluted commercial bleach were then used to clear the fragments of

chlorophyll and also the staining by digestive juices. Too strong a bleach solution resulted in bubbles emanating from the gut specimen. The bleach also enabled the fragments to be spread evenly over the whole slide, to facilitate the identification of all fragments. The slide was scanned systematically several times under a binocular microscope to identify the fragments. No staining of the gut sample was found to be necessary. Analysis of hind-gut in addition to crop added little to the time taken to complete each sample, once familiarity in identifying fragments had been achieved.

Most identifications were completed under a magnification of 120 diameters although magnification of 240X was also used when greater detail was required. Identifiable fragments consisted of a few to several hundred epidermal cells, of total dimensions between about 0.01 and 3.0 mm.

The plant species were recorded in decreasing order by optical estimation of the abundance of fragments. Where fewer than five fragments of a species occurred, the species was recorded as a nibble and not used in the analysis of data on diet. The contents of the crop and hind-gut were recorded separately but combined as one sample for the analysis of results. Thus the assessment of the ingestion incidence of food in the present study is largely of a qualitative nature.

The species ingested, together with the age, sex, species, sampling collection time, and plot of collection of the grasshoppers were recorded on a card index system for later

analysis, together with miscellaneous data including a count of the external Erythreid (unnamed species) mite parasite present on each individual.

CHAPTER 6

RESULTS OF EPIDERMAL ANALYSIS

INTRODUCTION

Scope of Investigation : Material Analysed

The food contents from a total of 1642 grasshoppers were examined in the main analysis, collected from 19 plots. Of these, 1400 were adults and 242 included juveniles of all instars. The four grasshopper species were represented in proportions according to the following table:-

TABLE 5

Summary of Grasshopper Numbers Examined by Epidermal Analysis

	Adult	Juvenile	Total
Brachaspis nivalis	390	92	482
Paprides nitidus	581	64	645
Sigaus australis	390	83	453
Sigaus villosus	59	3	62
	1400	242	1642

These figures represented the combined totals from the three grasshopper collections made in the summer 1968/69, and the further restricted collection from January 1970.

The grasshoppers were analysed with respect to plot and period of collection, species, sex, and age class. However because of the diversity of feeding revealed, the collecting times, and juveniles of all instars, were combined respectively for the analysis of results in order to bulk numbers within various classes. A breakdown of all numbers analysed by taxonomic, adult sex, and summarised age class groups for each plot, appears in Table 6.

The collection of grasshoppers, and preparation of material for analysis has already been described in Chapter 5.

Assessment of Food

The contents of grasshopper guts were found to consist mainly of plant material. Fragments of leaf origin were generally identifiable to species, and included the major part of the diet. This included both monocotyledonous and dicotyledonous species as well as fragments from ferns, mosses and lichens. The presence of moss and lichens were recorded and used in the analysis of grasshopper diet, although only the most significant moss species, Polytrichum juniperinum, was identified. Grasshoppers from the collections made later in the season were also found to include a considerable content of fragments of flowers. These were recorded

TABLE 6

Numbers of Grasshoppers Analysed, by Plots

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	TR	A3R	Sub totals	Totals
Plot Totals	56	104	99	80	125	99	86	73	88	37	129	30	86	153	107	43	154	51	51		1822
B. nivalis																					
Adult : male	-	9	1	18	9	13	-	13	13	3	1	-	22	18	-	11	20	12	14	177	
female	-	26	-	20	12	20	-	27	22	8	1	-	21	22	-	2	18	7	7	213	390
Juvenile	-	18	-	11	5	6	-	-	3	2	-	-	15	7	-	1	7	16	1		92
Total	-	53	1	49	26	39	-	40	38	13	2	-	58	47	-	14	45	35	22		482
P. nitidus																					
Adult : male	16	13	18	4	26	13	19	8	25	6	28	8	1	26	27	7	19	2	-	266	
female	16	9	26	9	24	25	21	8	19	6	37	9	8	33	27	5	33	-	-	315	581
Juvenile	5	8	13	1	3	2	6	-	6	2	6	-	1	3	6	1	1	-	-		64
Total	37	30	57	14	53	40	46	16	50	14	71	17	10	62	60	13	53	2	-		645
S. australis																					
Adult : male	6	3	9	3	16	5	9	2	-	4	16	5	1	10	20	5	21	1	-	136	
female	4	7	29	12	19	12	30	5	4	6	22	8	16	7	24	9	19	1	-	234	370
Juvenile	9	9	3	2	11	3	1	-	-	-	17	-	1	9	3	2	13	-	-		83
Total	19	19	41	17	46	20	40	7	4	10	55	13	18	26	47	16	53	2	-		453
S. villosus																					
Adult : male													1	6				3	18	28	
female													1	11				8	11	31	59
Juvenile													-	-				1	2		3
Total													2	17				12	31		62

from between 20 and 80 percent of individuals on plots in the January 1969 sample. Apart from the flowerparts of Anisotome aromatica, and fruit of Gaultheria depressa which were both common and easily recognisable, the reproductive parts were not identified but recorded merely as flowerparts of monocotyledons or dicotyledons. These totals were later used in the analysis of grasshopper diet.

A small proportion of specimens were found to contain empty guts, usually as a result of being captured freshly moulted, ovipositing, in copula or senescing. These grasshoppers were also incorporated into the overall analysis of the diet.

A further small proportion of grasshoppers were found to have consumed insects. These fragments were not identified to species, although their presence was noted. The incidence of insects was not incorporated into the overall analysis of grasshopper diet.

Presentation of Data

The raw data on food consumption by the grasshoppers was summarized on the basis of the total incidence of individual components of the diet for the various grasshopper classes within each plot. These details of total numbers of all food items occurring in grasshopper classes by species, sex and age classes for each plot appear in Appendix B. Juvenile classes were aggregated as one age group.

The total numbers of the plant species ingested were converted to frequencies in order to obtain a picture of the relative importance of each in the grasshopper diet, and to observe the manner by which ingestion related to the composition of the vegetation, to grasshopper species and classes, and to the time of season. To observe these effects an extensive comparative analysis of the results was made both on an inter- and intra-plot basis.

RESULTS: A - RATE OF INGESTION AND DERIVATION OF FREQUENCY VALUES

Rate of Ingestion (IR)

The rate of ingestion refers to the number of plant species recovered from each grasshopper, and gives an indication of the feeding pattern of grasshopper species. A predominance of one food item in the gut indicates that the species feeds largely on one species during a given feeding period, while a greater number indicates a multiple feeding habit.

It was found that the grasshoppers in the present study as a rule contained more than one species of plant present in the gut. This reflected the pattern of multiple feeding behaviour determined from field observation. The number of species ingested per grasshopper varied widely, from one plant species to a maximum of eight recovered from to individuals.

The distribution of species recovered from all adult grasshoppers is given in the following table:-

TABLE 7

Distribution of Plant Numbers Recovered per Adult Grasshopper

No. of plant species per grasshopper	0	1	2	3	4	5	6	7	8	9
% of grasshoppers	1.5	19.8	30.0	24.7	15.4	6.4	1.8	0.3	0.2	0.0

The average number of plants represented per grasshopper was found to vary between plots, and between grasshopper species and sex. The average rate of ingestion for grasshopper classes within each plot were calculated as follows:

$$\text{Ingestion Rate (IR)} = \frac{\text{total no. plant ingestion recordings}}{\text{total no. grasshoppers}}$$

The ingestion rates of adult grasshopper classes in plots are presented in Table 8. Because of the individual variance in ingestion rates, calculations were made only in categories represented by ten or more grasshoppers. It is seen that the combined ingestion rate varied widely, from 1.9 to 3.4 between plots. Male grasshoppers appeared to have a lower rate of ingestion than the corresponding females, and P.nitidus a lower rate overall than the remaining species. However an analysis of variance between the sexes of each species, and between the combined ingestion rates for grasshopper species did not show

TABLE 8

Average Ingestion Rate* for Adult Grasshoppers within Plots

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	TR	A3R	Mean
B.nivalis																				
male	-	-	-	2.3	2.7	2.9	-	2.5	2.7	-	-	-	2.0	3.3	-	1.8	1.6	3.0	2.1	2.4
female	-	2.4	-	3.5	3.0	3.3	-	2.7	2.0	-	-	-	3.3	2.8	-	-	2.4	-	-	2.8
combined	-	2.7	-	2.9	2.9	3.2	-	2.7	2.3	2.8	-	-	2.6	3.1	-	1.9	2.0	2.8	2.5	2.7
P.nitidus																				
male	1.7	1.8	2.7	-	2.2	1.6	2.7	-	2.1	-	2.3	-	-	2.1	1.6	-	1.5	-	-	2.0
female	2.4	-	3.5	-	2.5	2.6	2.7	-	2.5	-	2.7	-	-	2.6	1.9	-	2.4	-	-	2.6
combined	2.1	2.0	3.2	2.7	2.3	2.3	2.7	2.0	2.3	2.9	2.5	3.4	2.6	2.4	1.7	2.7	2.1	-	-	2.5
S.australis																				
male	-	-	2.9	-	2.6	-	2.9	-	-	-	3.7	-	-	2.9	2.1	-	2.1	-	-	2.7
female	-	-	3.2	2.8	3.4	3.0	3.1	-	-	-	3.6	-	2.4	-	2.6	3.1	3.0	-	-	3.0
combined	2.7	2.4	3.2	2.5	3.0	2.2	3.1	3.0	2.8	3.4	3.6	3.3	2.5	2.3	2.3	2.7	2.5	-	-	2.8
S.villosus																				
male														-				2.9	-	2.9
female														3.0				2.7	-	2.9
combined														3.2				2.8	2.8	2.9
Whole plot including juveniles	2.3	2.2	2.9	2.6	2.6	2.6	2.6	2.6	2.2	3.4	2.7	3.4	2.6	2.6	1.9	2.4	2.1	2.9	2.7	2.6

* Ingestion Rate = no. of plant species recovered per grasshopper

significance at the 95% level of confidence, and only the difference between S.australis and P.nitidus was significant at the 90% level.

The variation of ingestion rates between plots was also found to be insignificant when statistically analysed, and little can therefore be concluded regarding the relationship between IR and plot. The floristic abundance of the plot and the density of the major physiognomic dominants Chionochloa pallens and Celmisia lyallii appeared to have some influence. Open plots with an abundance of low growing species or shrubby plants (C2V, A1O, A2V2), were generally conducive to a higher IR value than those which were floristically poor (A4V, A4O, A5O), or where dominants formed a very dense cover (C1V, A1V).

Expression of Frequency of Ingestion

Because the grasshoppers were of multiple feeding habits, the ingestion of plant species may be expressed by frequencies in two ways as follows:

(i) on the basis of the frequency occurrence of food items in grasshoppers as a proportion of all grasshoppers in the sample i.e. the grasshopper ingestion frequency (Gf). Thus for a given plant species A,

$$\% \, Gf = \frac{\text{no. ingestion recordings on plant A}}{\text{total no. of grasshoppers}} \times 100$$

(ii) on the basis of the frequency occurrence as

a proportion of the total food selections made by grasshoppers i.e. the food ingestion frequency (I_f). Then for the given plant species A,

$$\%I_f = \frac{\text{no. ingestion recordings of plant A}}{\text{total no. plant ingestion recordings}} \times 100$$

I_f may also be obtained from G_f, by dividing this figure by the ingestion rate,

$$\text{e.g. } \%I_f = \frac{\%G_f}{IR} = \frac{\dfrac{\text{no. ingestion recordings of plant A}}{\text{total no. grasshoppers}} \times 100}{\dfrac{\text{total no. of plant ingestion recordings}}{\text{total no. grasshoppers}}}$$

The significance of this enunciation is best seen when compared to that for the analysis on pages 92 - 94. It is observed that both V_f and I_f express an absolute frequency for the plant species and are therefore directly intercomparable. The selection of food by the grasshoppers is more readily comparable with that of the abundance of vegetation when expressed in this way. Furthermore, for what is essentially a qualitative rather than quantitative investigation of grasshopper food selection, the ingestion frequencies of grasshoppers from different plots, and of different species, age or sex categories appeared to be made more comparable on this basis of ingestion frequency. Although the differences in the number of species ingested were not statistically significant between these classes, they were considered too great to be neglected.

Hence results involving feeding frequency were based on I_f values.

Quantitative Measure of Food Intake

The data, as analysed for this study, strictly represents a qualitative analysis of food selectivity of the grasshoppers since no account was made for the intake of each plant on a quantitative basis. Food selection by grasshoppers appears to be largely on the basis of making contact with a plant, thence staying to feed, or leaving for another plant. Therefore each species recovered from the gut was the result of an independent selection, which was influenced by the acceptability of the plant species, and its abundance in the vegetation.

The patterns of food intake, in terms of the absolute amounts of species ingested, were therefore likely to be of a similar nature to the patterns of feeding revealed from the ingestion frequencies, although the real differences between favourable and unfavourable species would probably tend to be underestimated by these values. This is because not only can a favourable species be expected to be consumed more frequently in relation to its abundance than an unfavourable species, but more of it is likely to be ingested at each feeding contact with the plant. As the trends observed in the qualitative analysis of feeding selectivity are probably accentuated in real terms, there may also be a correspondingly greater differential impact on components of the vegetation.

B - FOOD SELECTION WITH RESPECT TO VEGETATION

In order to gain an indication of the relationship between grasshopper feeding and the vegetation, the combined results of all grasshoppers were compared on a plot basis. The expression of results in this manner enabled the contribution of the various plant species to the total grasshopper diet to be determined. An indication of the extent of utilization of the vegetation by the grasshopper population was also indicated, by comparing the host range recovered from the grasshopper crops with plants available. The relative favourability of plant species for the grasshoppers was obtained from an analysis of the ingestion with respect to their availability as measured by their abundance in the vegetation. An elucidation of the more vulnerable components of the vegetation, by virtue of their acceptability to grasshoppers, may then enable some indication of the likely impact that unfavourably high populations could exert on the vegetation.

In combining the feeding results of all grasshoppers in each plot for this purpose, the assumption was made either that the grasshopper sample was representative of the population present on that plot, or that all grasshoppers exhibited similar feeding behaviour. By the random collection, as encountered, of grasshoppers during the sampling, it was attempted, albeit roughly, to satisfy the first criterion. The analysis of ingestion between grasshoppers also indicated that combined

analysis of results was also valid on the second assumption.

Utilization of Vegetation

The number of different species recovered from all grasshoppers within each plot was compared with that of the floristic composition of the vegetation and is illustrated in Figure 4. The recovery of plants from grasshoppers was depicted in the figure in respect of the number of grasshoppers analysed for each plot. These comparisons revealed that a very high proportion of the plants in the vegetation were utilized by the grasshoppers. The floristic abundance for each plot ranged between 60 and 19 species, of which between 43 and 17 were recovered from the grasshoppers. As the floristic abundance of the plots increased, a larger proportion of species failed to be recovered from the grasshoppers. This no doubt coincided with an increase in the number of very minor species present in and around the collection sites. The failure of such species to be ingested was therefore more the result of their small chance of being contacted by feeding grasshoppers than their unacceptability.

With regard to the numbers of grasshoppers analysed for each plot, it was observed that when less than 80 grasshoppers were analysed, the number of species recovered fell rapidly, and that about 100 or more grasshoppers were required in order to gain a reasonably consistent rate of recovery of plant species. These results indicate the very general and diverse

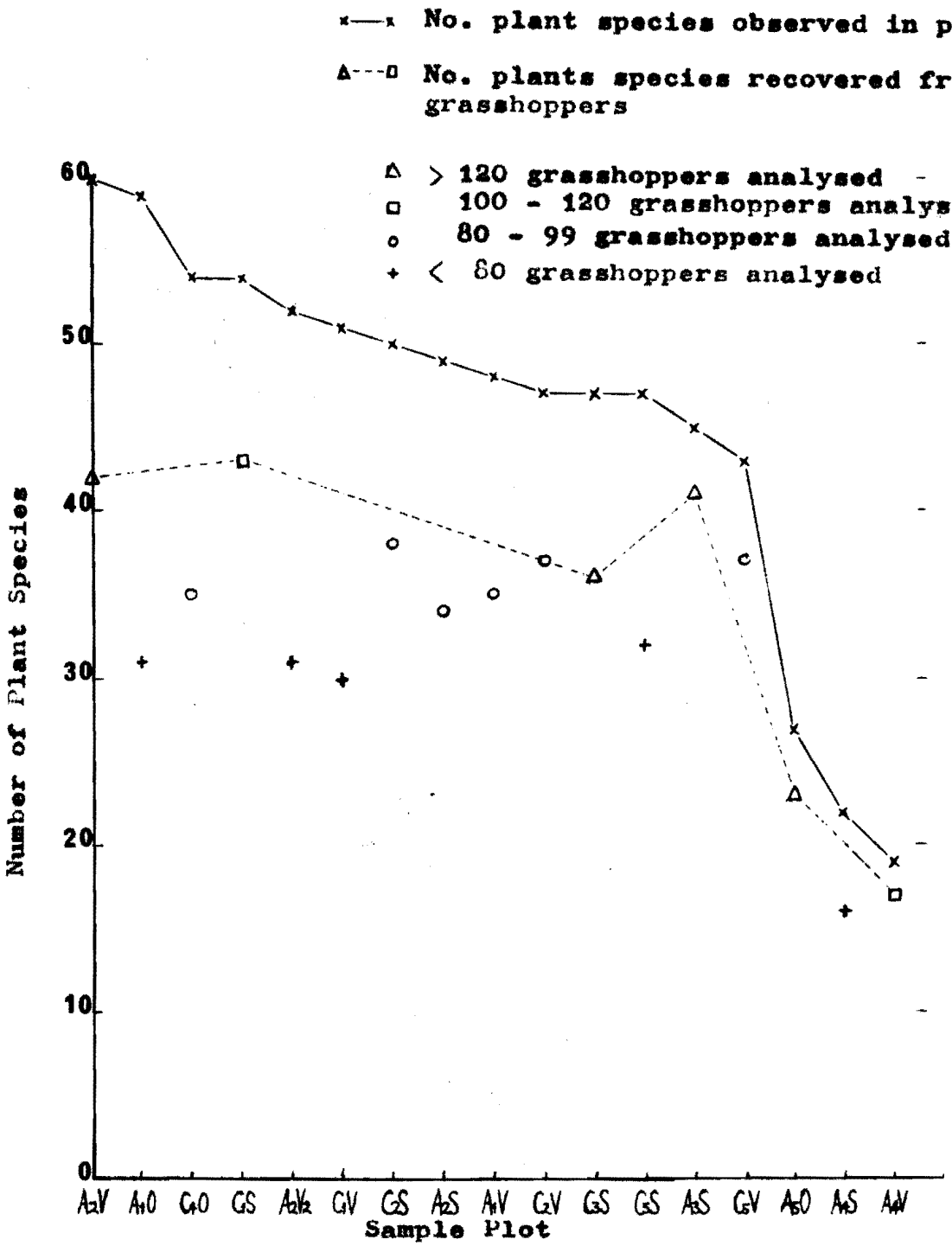


FIGURE 4

Floristic Utilization of the Vegetation by Grasshoppers analysed from Each Plot

pattern of food selection of the grasshoppers.

Table 9, although principally comparing the ingestion frequency of plant species with their abundance in the field plots, also reveals the high degree of utilization of the vegetation by the grasshoppers. Of those plants which were contacted during point analysis of the vegetation from any plot, only nine species (less than 10%) failed to show up in the grasshopper analysis. These species represented an insignificant portion of the vegetation (much less than 1%) and were generally recorded from one or a few plots only. Their lack of recovery was therefore the result of the low chance of contact by grasshoppers. This conclusion was exemplified by a further ten species which were recovered from grasshoppers, but which were not contacted during point analysis. These were again from plants which were of very minor abundance, and which contributed to a negligible part of the total grasshopper diet. Seven of the species were obligative scree growing species recovered from B.nivalis, and which did not come under vegetation analysis.

It was observed that no major species in the vegetation failed to be represented in the grasshopper analysis. There was no indication that any plant was entirely avoided by the grasshoppers and it was concluded that the host range is one o ubiquity among the plants in the natural environment of the grasshopper populations.

TABLE 9

Ingestion Frequency (above) by Grasshoppers, and Vegetation Frequency (below), of Plant Species from Study Plots, and Overall Favourability Index Ratio of the more Important Plants Ingested by Grasshoppers.

	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	Total	Ratio
MONOCOTYLEDON																			
Agrostis dyeri		1	1	1 t					t	 t								3 1	
Agropyrum scabrum		1 t		1	1				2	1 t								6 1	
Anthoxanthum odoratum										t									
Astelia nervosa													1	1 t				2	
Chionochloa crassiuscula											1 7	1 16		1	9 19	7 5	1 1	21 48	0.4
C.flavescens									t										
C.oreophyla												5 20		3				8 20	0.4
*C.pallens	5 52	3 36	1 21	1 19	1 15	1 34	1 28	2 18	3 52	4 19	1 29	 4	t 3	 13	t 28	2 35	2 26	28 432	0.1
Deyuxia avenoides						t				t							t		
Erythranthera pumila		3							2									5	
Festuca rubra						t			t t										
F.novae-zelandia		t	t			2 5							t					2 6	0.3
Hierochloe fraseri	1	t t																1	
Lachnagrotis forsteri	5 1	2 1	3 t	1 1	2 1		5 1	2 1	3 1		1 t	1 t			4 t	4 t	3 1	36 10	3.6
Luzula pumila												1 t	2	1 1	1			5 1	)
L.rufa	2	4 t	6 t	5 1	4	6 2	5 t	4 1		3 1	3 1	5	2 t	2 1	t	2	 t	53 9	) 6.2
L.traversii	2	2			t													4	)
Microlaena colensoi			t				t	1	t		1 t	2						3 3	1.0
Notodanthonia setifolia		t t			3				t	1 1	t		1 4	2	t	8 16		11 27	0.4
Poa colensoi	8 8	9 10	5 5	9 9	5 16	4 11	5 6	3 7	8 1	6 3	10 7	9 6	8 4	8 13	6 6	9 13	12 9	124 136	0.9
P.mackayi	t	t 1	2 1	1 t	2		4 t	1	9 2	2 1	1	1		2 t	2 1	1		27 8	3.4
P.sclerophylla																	t		
Rostkovia gracilis			1							1	2	2 6		t 1			t	5 9	0.6
Uncinia caespotosa	1 1		t	t t	1	t 1	2 t	1	2 1		3	3	t	2	2		2	20 5	4.0
Trisetum youngii	t	t	t						2 t									2 1	

* also includes C.rigida and C.macra

Table 9 (cont.)

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2VO	A20	A3S	A4V	A40	A50	Total	Ratio
DICOTYLEDON																			
Acaena spp.	2 1																	2 1	
Aciphylla squarrosa	t					t	t		1 4	1								1 6	
Aciphylla monroi		t			2 9	t t		1 1		1	4 3	1 2	1 1	6 3	9 5	6 4	1 1	31 30	1.0
Anisotome aromatica	5 1	8 4	5 8	6 2	2 1	2 1	10 11	5 9	t	3 7	11 5	18 8	7 6	4 1	1	4	6 5	97 68	1.4
Anisotome filiforme			t	t t	t		1		1 1									3 1	
Brachycome sinclairii		t				t							1	1				2 1	
Cardamine spp.	t	t	1		2		2 t		1					1	1	2		10 1	10.0
Celmisia discolour											t 1								
C.dubia												1 2							
C.du-rietzia		t 1					1	1 t			1		1					4 1	
C.gracilis						t													
C.laricifolia	1				1		t	2		1	6 4	4 2	4 3	2 t				19 12	1.6
C.lyallii	5 12	4 20	5 10	5 34	4 25	t	4 7	1	5 18	2	1 6	1	t	3 29	13 29	5 22	11 23	66 240	0.3
C.sessilifolia											1	4 2	2 1					7 3	2.3
C.spectabilis		t	8 2	1 1	2	6 16	3 4	3 4		3 11	6 2	1 1	2 1	1 1				36 43	0.8
C.viscosa	1	1	3 10	3 2	8 4	1 1	4 12	2 9		2 1	8 16	6 10	4 1	10 6	11 t	10 10	5 2	79 94	0.8
Colabanthus acicularis						1				t				t				1	
Coprosma cheesemanii	1		t t	3		2	t	1		7	t	3 1	3	2				15 9	)
C.pseudocuneata			t	1						4 2			t	t				6 2	) 2.9
C.pumila			7 5	10 1	1		t	8 6			t	5	3 2	1				36 9	)
Cotula atrata		t						2										2	
C.pyrethrifolium		t 2	t 5	t	t					1 3	t			1				4 10	
Cyathodes fraseri						1 3												1 3	
Dracophyllum pronum		1	3	1 1	2 4	1 1	t 5	18		2	3 6		9 57	2 6				19 102	0.2
Drapetes deiffenbachii			3 8				t	t			11 4	6 3	9	3				32 16	2.0
Epilobium crassum								1						t				1	)
E.pedunculare	1	1	2	2			1		1	2 t	2	1	3	2				16 2	)
E.perplexum	t 1	2	t		3 1		t		3	1	1		3	1			1	13 4	) 3.5
E.pycnostachyum					1	t												1	)
E.rubrum		2 t		t 1	1 t	t 2	t	1	2 2	3 1	1	1		t	1	1	1	15 7	)

Table 9 (cont.)

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	Total	Ratio
Euphrasia spp.		t	1 1			t t	3 t	4 t					1					8 8	
Forstera tenella				t			t t	t											
Galium perpusillum		1																	
Gaultheria depressa	11 5	7 5	8 7	4 7	5 2	2 2	9 7	4 2		4 5	1	2 2	8 4	3				68 48	1.4
Gentiana corymbifera			1 t	t 1	4 2	3 t	3 1	3 t			3 1	3 1	t	4 1	1	1 t	1	27 9	3.0
Geranium microphyllum	7 2	1 1	t				t t		t	2								11 3	3.7
Geum uniflorum	1 1		t															1 1	
Gnathalium traversii									t										
Haastia sinclairii						1							1 1	2				4 1	
Hebe cheesemanii		t				t			t	t				t				1 1	
H.epicradea		1		2				2	t									5	
H.lycopodiodes		t t	t t		1		1 2	1		3				t				7 3	
H.pinguifolia	t	3 1	2	2 t	6 5	10 4	t t	2 t		3 14			5	1				34 25	1.4
Hellichrysum bellidiodes										t									
Leucogenes grandiceps		t				3 t			t	t			t	1				5 1	
Meuhlenbeckia axillaris				t						1 4								1 4	
Myrsine numularia			3																
Oreomyrrhis colensoi	t								1										
Ourisia caespotosa		1	1	t 1	t			1			t	1 t	t					3 4	
O.sessiliflora												1 t	1	1				3	
Phyllachne colensoi			t	1	2		2	3			t 1	t	2	2				14	
Pimelia prostrata		t t				t t	1												
Pittosporum crassicaule										2 1			1						
Pinus spp.							t 1	6 1										6 2	
Plantago novae-zealandiae		t	2	t	t				t	5	t	3 1	t					11 2	5.5
Pratia angulata	1 1	3 1	3 2	t 2	5 3	3 2	4 t	1 1	t	1	t	3		1 1	9 1	5 2	11 5	47 27	1.7
Pygmea pulvinaris													1 1					1 1	
Ranunculus ensyii	1	1 1	5 1	1	5		t t	2 1	4 t	12 3	t		t					32 7	4.6

Table 9 (cont.)

	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	Total	Ratio
Ranunculus haastia								3											
R.insignis	t																		
R.serriciophyllus											t								
Raoulia bryoides						1													
R.grandiflora	1		1		3 1	2 t	1	1	2		1 1	1	1	3 3	2 t	4	4 2	26 9	2.9
R.subsericea		t				1 4												1 4	
Raoulia hybrid spp.						t													
Rumex acetosella	3	5		t		3 1			1	1								13 1	13.0
Schizeilema spp.	1 1	1								1	1							2 3	
Senecio lagopus	t	1	t 1	1 t	t		1 2	2 3		1	2 t		5 2	1 t				14 10	1.4
Senecio scorzoneroides		t	t		t							1							
Stellaria gracilenta			t						3										
S.roughii						1 1		3											
Taraxicum magellanicum	1	1			2			t	t	t								4 1	
Wahlembergia albomarginata	1	4 1	4 1	9 1	2 1	6 1	2 1	6 2		3 1	1 t		3	2		5	t	48 9	5.3
Viola cunninghamii	1 t	1 1	1	1 t	2 1	1 1	t t	1 1	1		1 t			4			1	14 6	2.3
flower - -Dicotyledon	14	8	6	8	13	16	8	12	8	14	4	7	10	8	6	8	2	160	
-Monocotyledon	2	t	t		2	1	2	t						2	t	4	2	16	
-A.aromatica	3	1	2	t	2		5	1	t	3	3	2	2	5	11	17	6	64	
fruit -G.depressa	3	8	2	3	t	6	2	3										27	
unidentified - Dicotyledon			t		1	3		1	1	1	1			t				9	
Monocotyledon		3			t				4		t				t	1	t	9	
SPOROPHYTE																			
Blechnum penna-marina	4	1 4	2 t	3 6			t		20 13	4 3		1						30 32	0.9
Hymenophyllum villosum								t											
Lycopodes australianum					t						t t								
L.fastigiatum	2 3	t 1	7 5	2 2			t 1	1 1	3		t 1	t	t					16 15	1.0
Polystichum cystostegia				2 1					1								2	5 1	

Table 9 (cont.)

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	Total	Ratio
Polytrichum juniperinum	3	4	1	1	2	4	5	2	4		2	2	2	4	7	5	8	54	1.2
	t	1	t	2	3	2	1	4	2	5	1	1	3	4	8	4	3	45	
Unidentified - Moss	1	1		1	1	2	t	1	t			1	1	1	1		2	13	
- Lichen	t													1	t				

Relative Acceptability of Plant Species to Grasshoppers

The comparison of the ingestion and vegetation frequencies in Table 9 enabled the selection of food to be examined with respect to its availability. An indication of the relative preferences of the grasshopper population for plant species may be obtained from the rates of sum totals of I_f and V_f values for the plots. The value obtained thus provides a favourability index for the plant species.

i.e. Favourability index (FI) = $\frac{I_f}{V_f}$

Value of less than unity indicated that these plants were selected at a level below their abundance in the vegetation while those above unity indicated a rate of selection above that of its occurrence in the vegetation.

The actual value of FI may be influenced by two factors in the present study. The first and most important of these is that of the inherent favourability of plants to the grasshoppers, the second could occur from a bias in the results due to an interaction between the growth habits of the plants and the feeding habits of grasshoppers. Grasshoppers were observed to carry out feeding behaviour predominantly by searching for food at ground level. In this case low growing, prostrate and rosette species could tend to show a higher FI rating relative to the tall dominant species, for which a proportion of the vegetation analysed by the point method consisted of aerial canopy not readily available to

grasshoppers. However any bias introduced by this means was minimized by assessing vegetation frequency from the first hits on each plant species only. The tall species were frequently multilayered and had components close to the ground level as did lower growing species. No consistency in favourability could be determined as a result of growth habit alone, and both tall and low growing species were included among species of high and low relative favourability. Therefore FI values were concluded to be largely the result of operation of inherent preferences for food plants by the grasshoppers.

The favourability index was calculated in Table 9 only for the more important species. The plant species concerned were seen to divide into several rather distinct groups with regard to the favourability rating, which are included below:

(i) those of low favourability (FI = 0.1 - 0.4).

These species were few in number among those analysed, but significantly they included species which contributed greatly to ground cover. Chionochloa pallens was the least favoured of all species as food for grasshoppers. However this species probably more than any other factor apart from that of aspect, influenced the distribution and abundance of grasshoppers within the confines of their alpine environment. Other grass species which fell into the low favourability category were the other Chionochloa species, Notodanthonia settifolia and Festuca novae-zealandiae. Of the forb species only Dracophyllum pronum and Celmisia lyallii were included. However although C.lyallii

had a favourability rating of 0.3, its second rating to Chionochloa pallens in vegetation abundance gave it a ranking of fifth in the overall ingestion frequency by the grasshoppers. Dracophyllum pronum commonly formed extensive cover, providing open sunny situations for grasshoppers. Large numbers of early instar grasshoppers, and often gravid females were frequently observed to be in association with large open patches of this plant.

(ii) plants of medium favourability (FI = 0.8 - 1.2). Since these species were selected on a level about equivalent to their abundance in the vegetation, these indicated some neutrality in preference for them by grasshoppers. This group included all the lower taxons, e.g. the cryptogams (Blechnum penna-marina and Lycopodium fastigiatum), and moss (Polytrichum juniperinum), and also included Celmisia spectabilis, Celmisia viscosa and Aciphylla monroi among the forbs, and Poa colensoi among the grasses. This group again showed the characteristics of the first group of tough or nonsucculent leaf character, though generally to a lesser degree. Again the group included species which together contributed in large part to the total vegetation cover.

(iii) species of high to marked favourability (FI = 1.4 and above). This group included the majority of species numerically and were characterised in both monocotyledonous and dicotyledonous types by their general succulence compared to the above groups. The species

individually were generally of more minor importance in the vegetation cover, although some of the species were present with a high degree of constancy within plots e.g. Anisotome aromatica, Gaultheria depressa, Pratia angulata, Wahlembergia albomarginata and Luzula rufa. Some of the species had favourability ratings up to about ten, although data for some of these species was sparse, reflecting their low level of occurrence in the vegetation. Some of the highly favoured species e.g. Cardamine and Luzula rufa, were seldom seen without severe grasshopper damage by late summer. It is not known if, or to what extent the low abundance of such species may in fact be the result of the intensity of grasshopper feeding.

Although the relative values of FI help to reveal those species, or components in the vegetation which are most vulnerable to grasshopper attack, it does not necessarily follow that these species are most prone to overexploitation when grasshopper numbers are unfavourably high, or that their exploitation is of greatest significance to the state of vegetation cover in the long term. The relative impact of grasshopper feeding is also influenced by the plant growth habits. For instance the effects of a moderately severe amount of feeding may have less impact on a rapidly growing species, whose leaves die back each year, that a smaller amount of feeding on a slow growing perennial, where the effects of grasshopper feeding may be cumulative over a period of ten or

more years, considered to be the turnover rate for such vegetation by Nordmeyer (1966).

Relative Contribution of Plant Species to Total Diet

By comparing the ingestion frequency values of a plant species with those of the others in the same plot (Table 9), an indication may be obtained of its relative importance in the diet of the grasshopper population regardless of its abundance in the vegetation. Similarly an indication of the relative contribution of plant species to the grasshopper diet in the whole area may be gauged from the sum of all plot If values. In this respect it was observed that a significant portion of the total diet selected was contributed by flowerparts, then in descending order of importance, Poa colensoi, Anisotome aromatica, Celmisia viscosa, Gaultharia depressa, Celmisia lyallii, Polytrichum juniperinum and Luzula rufa. Each of these species averaged more than 3% of the total selected diet. The fact that these species included four dicotyledonous species (both woody and herbaceous), two monocotyledons (a grass and a sedge) and a moss is further evidence of the very general nature of grasshopper diet selection.

Influence of Vegetation Abundance on Ingestion Frequency

The manner by which grasshopper ingestion of plant species responded to the abundance of the plant species in the

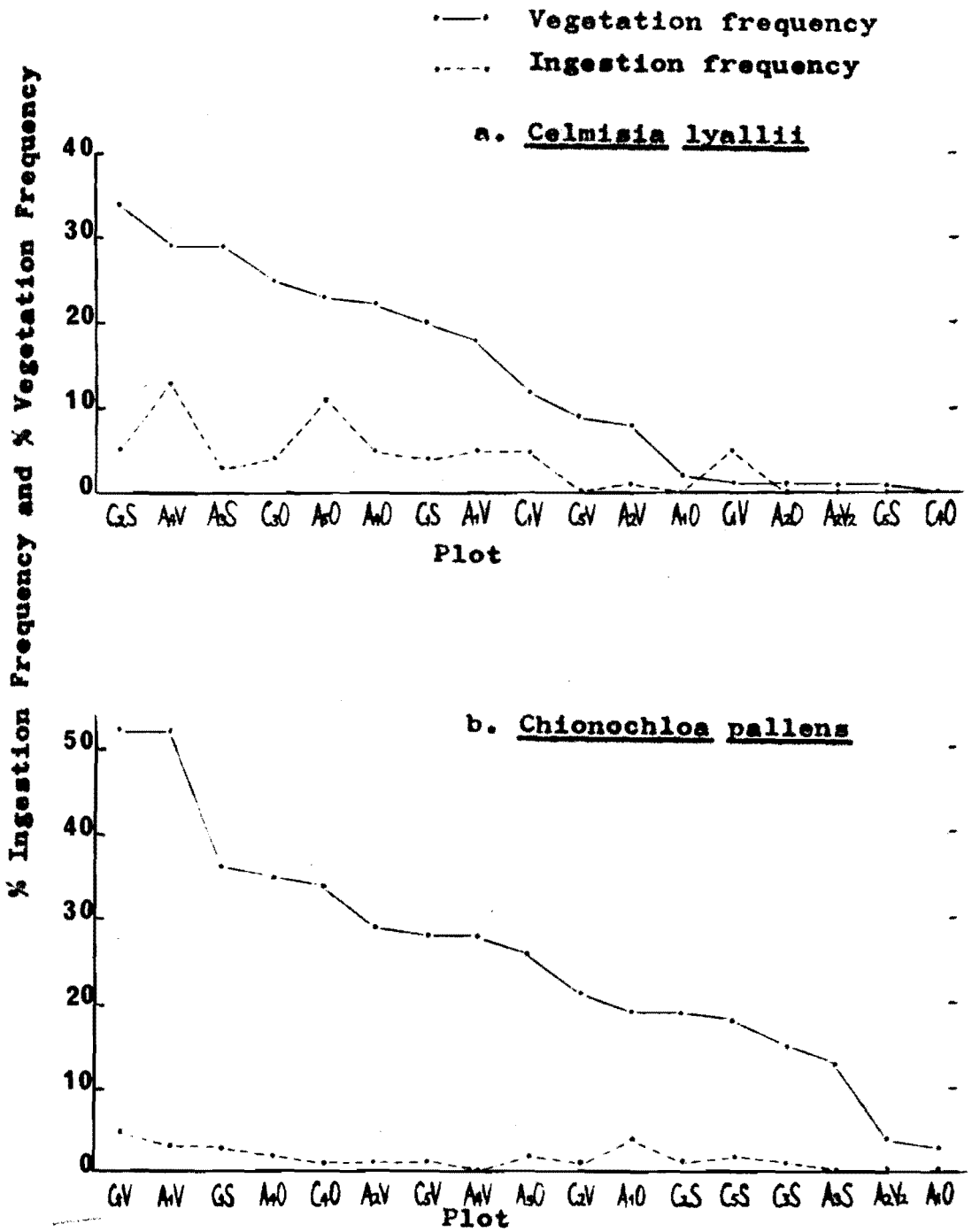


FIGURE 5
Frequency of Ingestion of selected Plants by Grasshoppers in relation to Vegetation Frequency (Availability) in Plots
(i) Low Favourability Species

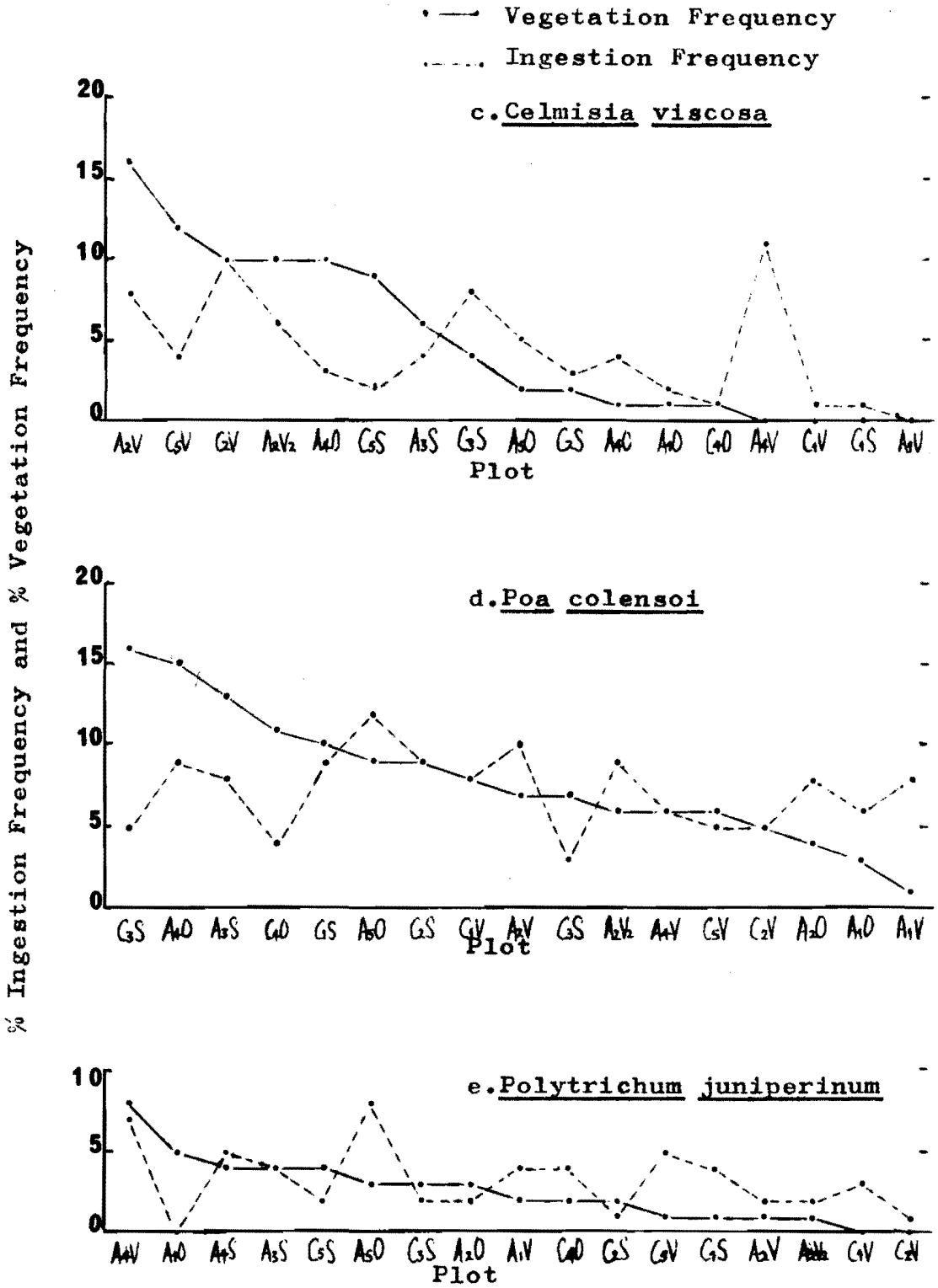


FIGURE 5 (contd.)

(ii) Medium Favourability Species

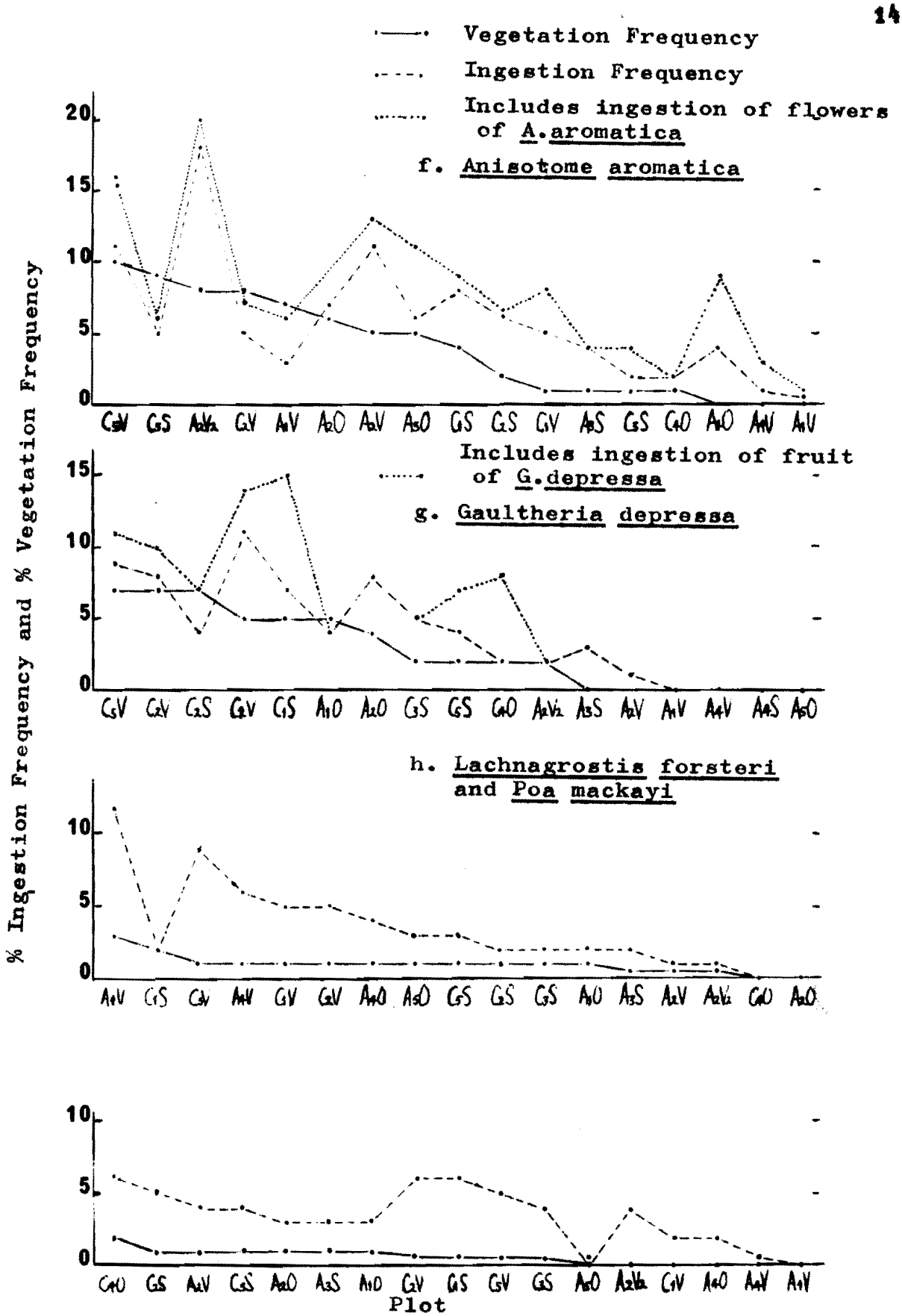


FIGURE 5 (cont.)
(iii) High Favourability Species

vegetation is best shown in graphical form, with the ingestion frequencies of the plants imposed on their vegetation frequency for each plot. In Figures 5 (a-i) this is done for several species within each of the main favourability classes. These selected examples were a generally typical representation of the interaction between vegetation abundance and grasshopper selection of the plants. The intake of the more unfavourable species tended to be reduced when more favourable species became readily available. However because of the overall abundance of less favourable species, their proportion of the total intake was, with some exceptions e.g. Chionochloa pallens, generally also high.

With regard to the low favourability class species (Figure 5 a, b) it is seen that consumption was generally at a constant, low level with respect to abundance, although dropping to zero consumption when the vegetation frequency fell to comparatively low levels, of about 10% depending on the actual favourability. The intake of these species was not therefore directly regulated by their abundance in the vegetation, but was a result of their own low favourability, and the availability of other species.

The second favourability group of species (Figure 5 c, d, e) reveal a similar pattern of selection to the first group except that their intake represented a higher rate in proportion to that available. Furthermore they were selected even at very low vegetation frequency levels, a feature not shared by the

first group. Satiation, or a more pronounced avoidance of these species therefore occurred when they were present at high frequency levels in the vegetation, and intake was not directly regulated by the plant availability.

With regard to the highly favoured species (Figure 5 f, g, h, i), these were shown to be consumed at levels fairly consistently above their abundance in the vegetation, even though the total level of intake might not be high. Consequently grasshopper ingestion of these species was more readily limited by availability, and a response in ingestion frequency to vegetation frequency is more evident.

In a similar graphical presentation, the contribution of the various components of the vegetation to the whole grasshopper diet may be seen in relation to their respective importance in the vegetation. In Figure 6 the results for various components of the vegetation are presented, with respect to the minor forb and grass species, which generally contributed most to the total grasshopper diet.

The plot order is presented in decreasing order of importance of the minor broadleaved plants in the vegetation. It is seen from comparing the graphs that these plants contribute most to overall grasshopper diet, and that they are eaten consistently above their level of abundance in the vegetation. The Chionochloa grass species contribute in a very minor way to the overall grasshopper intake, while being a major component of vegetation. Consumption of the remaining monocotyledonous

species occurs on a level at or about their abundance and largely reflect the presence of Poa colensoi. Utilization of the three major Celmisia species is at a low to moderate level, and below their combined presence in the vegetation. Non spermatophyte species generally occur at low levels in both grasshopper diet and vegetation.

Low forb content in the vegetation resulted in a slightly higher grasshopper consumption in relation to what is available, as well as some compensation from an increase in grass and Celmisia consumption.

In general summary, the average contribution of the plant groupings to both the vegetation, and grasshopper consumption are given below.

	Average Vegetation Frequency	Average Grasshopper Ingestion Frequency
Chionochloa species + Dracophyllum pronum	35	4
Other monocotyledonous species	13	19
Celmisia lyallii, C.spectabilis, C.viscosa	22	10
Moss and Fern species	5	7
Remaining dicotyledonous species) flowers)	25	46 14
	100	100

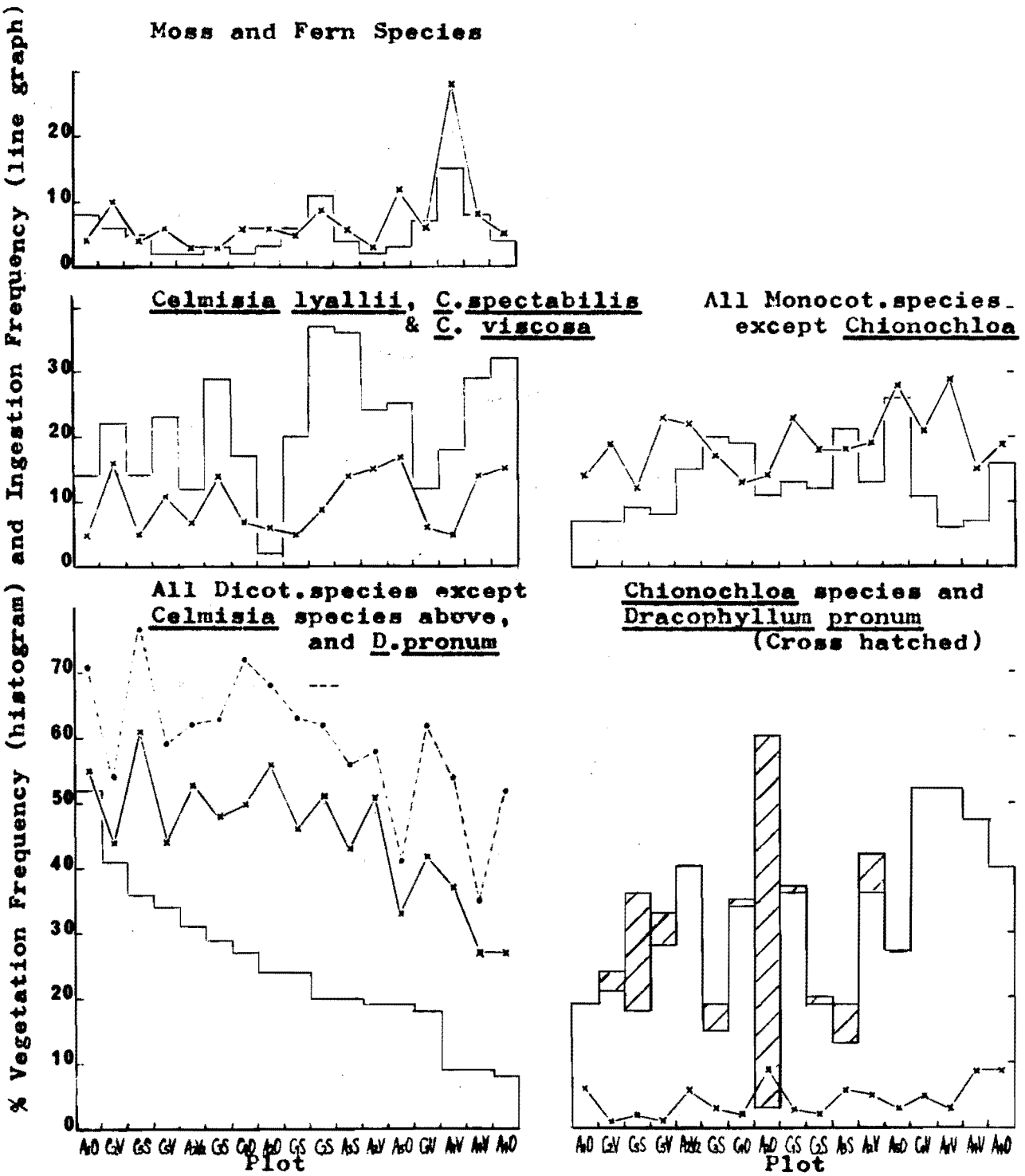


FIGURE 6

Contributions of Major Plant Categories to Vegetation Composition and Overall Grasshopper Diet in Plots

C - RELATIONSHIP BETWEEN INGESTION AND GRASSHOPPER SPECIES

The results as analysed in the previous section suggest that all the grasshopper species concerned were of similar, very general feeding habits, as now shown. It was found in section B that there was no indication of the complete rejection of any plant species normally available to the overall grasshopper population. A perusal of the individual plot records (Appendix B) further indicated that the complete ubiquity in host range applied to all the grasshopper species. However this did not rule out the possibility that the diets of the grasshoppers might differ, as a result of a "statistical selectivity" between the species.

An analysis to reveal possible differences in the food habits of individual grasshopper species was a necessary step before the pattern of feeding pressure exerted by populations of these species in other areas, could be defined from extrapolation of feeding data observed from the present or similar studies. If differences occurred in the selectivity between species, then feeding damage would then have to be related to the relative abundance of each species present in the areas under study. Further to this, an examination of the data for specificity in grasshopper feeding patterns could also reveal a degree of specialization, developed as a means of reducing interspecific competition for food. Such differences may be either the result of the expression of

inherent preferences which differ, or relate to the presence of plant species in relation to specialized preferential zones of occupation within general habitats.

With these view points in mind, the feeding data was re-examined in more detail with respect to the grasshopper species. The plant specificity index, and the relation between intake of grass versus forb species were criteria used by Mulkern (1967) to define the food habits of different grasshopper species. These were applied to reveal any differences in the general feeding behaviour between species of the present study, and an analysis of the selection of individual plant species by the various grasshopper species was carried out to reveal more subtle distinctions in selectivity.

Plant Specificity Index (P.S.I.)

The plant specificity index was calculated for the grasshopper species present in each plot, as the three-way mean of the sum formed from thrice the ingestion frequency of the most commonly ingested plant, twice that of the second favoured species, plus the ingestion frequency of the third. The results are presented in Table 10. The table shows that the overall means for the P.S.I. calculated from the individual plot values, were very similar for the three grasshopper species analysed, with values in the low twenties. Mulkern (1967) stated that P.S.I. values in the twenties were indicative of very general feeding habits. The fluctuation between the

TABLE 10

Plant Specificity Index of Diet for Grasshopper Species by Plots

	*PSI by plots																		Plot++
	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	TR	A3R	Mean
+Combined plot mean	20	17	13	19	13	16	18	14	26	22	22	23	17	18	20	19	23	-	-	19
B.nivalis	-	22	-	23	15	26	-	17	23	17	-	-	11	20	-	20	24	32	18	21
P.nitidus	23	21	20	32	21	18	18	31	38	24	22	23	25	19	34	28	29	-	-	25
S.australis	22	20	16	27	20	14	20	34	-	26	28	31	23	25	28	25	25	-	-	24

$$*\text{PSI (Mulkern, 1967)} = \frac{(\text{highest \% ingestion} \times 3 + \text{second \% ingestion} \times 2 + \text{third \% ingestion})}{3}$$

\+ determined from combined ingestion data for each plot

++ determined by averaging plot PSI values from the table

plots for individual species was probably a reflection of insufficient grasshopper individuals analysed in some of the categories. No strong relationship between P.S.I. and the composition of plots was discernable.

The plot means for all grasshopper species (calculated from summated plot ingestion data) was only slightly less than that for individual species, indicating that the diet, as well as the degree of diet selectivity, was essentially similar for the grasshopper species.

Grass Forb Index (GFI)

The grass forb index, as applied by Mulkern *et al* (1964, 1969) is of little value in defining the food habits of grasshoppers in the present study. The index is of greater value in classifying the feeding habits of grasshoppers of different subfamilies and resulting widely different feeding behaviour patterns, or where grasshoppers occurred which exhibited greater specialization in feeding. It has already been shown that the Craigieburn grasshoppers did not appear to select food on a taxonomical basis, indicated by the presence of both monocotyledonous and dicotyledonous plants in each of the favourability classes. The GFI would therefore be influenced by, and probably merely reflect, the relative quantities of the grasses and forbs available in the vegetation in the various favourability groups.

In addition, the GFI was devised largely with respect to

grasshoppers which contained only one species ingested at a time. In such cases the grasshoppers contained either a grass or a forb. In the present study both grasses and forbs frequently occurred in the same individual.

However observation of the differential rate of intake of grasses and forbs between grasshopper species could reveal differences, or similarities, in the selection for these two food classes. Therefore the ingestion of all monocotyledons, as a proportion of the total ingestion, were summarised in Table 11 as a means of observing the comparative intake of grasses and forbs. Although wide differences in the contribution of grasses to total diet of between 6 and 43 percent occured between plots, no significant differences were apparent between grasshopper species, the means for which were closely similar at about 20 percent. These figures would, on the basis of Mulkern's (1967) classification, place the grasshoppers as forb feeders, or mixed feeders preferring forbs. However it has already been indicated that, within the favourability groups, selection of individual plant species by grasshoppers in the present study is rather more influenced by its availability than by its taxonomic affiliation.

Diet Selectivity between Species

Ueckert (1968) and Hansen and Ueckert (1970) compared the diets of grasshopper species on Colorado rangeland on the basis of the similarity index of Sorenson (1948), which has been

TABLE 11

Proportion of the Diet of Grasshopper Species

contributed by Monocotyledonous Plants

	Contribution of Monocots as a % of total diet selections																
	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	Plot Mean
Combined plot mean	24	22	19	20	14	16	23	14	33	13	21	29	11	19	24	27	34	21
B.nivalis	-	22	-	23	11	16	-	13	43	20	-	-	13	21	-	20	39	22
P.nitidus	24	23	17	11	8	21	19	13	29	6	21	29	9	12	24	34	38	20
S.australis	23	21	20	18	23	7	27	24	27	9	21	28	10	36	23	26	26	22

employed largely by botanists in phytosociological work e.g. Daly, 1967. The similarity index is given as

$$\frac{2J}{a + b} \times 100$$

where, in the present situation J = number of plant species occurring in both of two grasshopper samples being compared.

a = number of species occurring in Sample A
b = number of species occurring in Sample B

However this index tends to overvalue the presence of rare species in the diet, relative to the dominant ones. The value of the sample therefore varies greatly with sample size, since the occurrence of the first plant species probably collects as fast as the analysis of individual grasshoppers, but subsequently new species are found much less frequently, although many individual grasshoppers may be analysed. Furthermore it has already been indicated that all the grasshopper species in the present study appeared to consume from all the plant species available to them.

A more satisfactory basis for the comparison of diets between species is the percentage of similarity (%S), based on a comparison of the makeup of the diets of two grasshopper samples in terms of the individual occurrence of the various plant species. As such, emphasis is placed on the more important dominant components of the diet. The value of the %S for a pair of samples is given by the summation of smaller values of the percentage ingestion of total individuals from

each sample. Thus for two grasshopper groupings A and B, with the following % composition of diet (modified from Southwood, 1966, P333):

		% Ingestion of Plant Species				
		a	b	c	d	e
Grasshopper Sample	A	25	42	10	23	0
	B	9	58	1	32	2

$$\%S = 9 + 42 + 1 + 23 + 0 = 75\%$$

The completed analysis of all such two-way comparisons between grasshopper categories is then presented as a matrix. Use of the similarity index and % similarity could be further extended to compare diet composition of grasshopper classes with that of the vegetation from which it was derived. This would enable a quantitative, comparative indication of the degree of specialization of diet selection by grasshopper classes.

Such analyses have not yet been carried out on data obtained for the present thesis. To find out if a statistical selectivity in the choice of food between grasshopper species occurred within the broad range of host plants available, the diet composition of individual grasshopper species was analysed. With the diversity of diet, and restricted numbers of grasshoppers examined from each plot, analysis on a plot basis would be meaningless. The combined totals of raw ingestion data from each plot were therefore used to calculate the respective ingestion frequencies. Table 12 shows the individual

TABLE 12

Diet Selectivity by Grasshopper Species and Sex

(% contribution to total intake by selected plants)

	% Ingestion Frequency								
	B.nivalis			P.nitidus			S.australis		
	♂	♀	Combined	♂	♀	Combined	♂	♀	Combined
Chionochloa pallens	2.1	1.6	1.6	2.3	1.2	1.7	0.0	0.1	0.1
Lachnagrostis forsteri	1.0	0.7	0.7	1.0	1.0	1.0	3.1	3.2	3.2
Luzula spp.	3.6	3.2	3.2	3.8	4.0	4.0	3.4	4.5	3.0
Poa conlensoi	7.2	10.2	8.7	4.4	7.3	6.2	7.0	7.4	7.5
P.mackayii	1.1	1.6	1.4	0.8	1.0	0.9	3.1	2.7	2.9
Uncinia caespitosa	1.1	0.5	0.7	1.7	1.6	1.7	2.0	0.9	1.3
Aciphylla monroi	0.3	0.4	0.3	1.5	5.3	3.8	1.1	1.9	1.7
Anisotome aromatica	2.2	4.5	3.5	2.5.	5.7	4.5	5.0	10.1	8.6
Celmisia lyallii	1.0	2.7	1.9	5.3	8.4	7.3	1.4	3.6	3.0
C.spectabilis	0.6	1.8	1.2	2.5	4.3	1.0	0.8	4.0	3.0
C.viscosa	1.4	5.9	4.0	2.7	5.0	4.1	6.4	6.5	6.7
Coprosma spp	5.2	2.7	3.6	3.4	2.4	2.9	1.1	1.3	1.3
Epilobium spp	5.8	4.5	4.9	1.9	1.5	3.2	3.9	2.2	2.9
Gaultheria depressa	4.4	1.3	2.4	6.8	4.8	5.6	3.1	3.0	3.1
Gentiana corymbifera	0.3	0.2	0.2	5.5	3.7	4.4	0.3	0.3	0.3
Hebe spp	8.3	4.1	5.6	3.6	2.8	3.2	0.6	1.0	0.9
Pratia angulata	2.3	3.1	2.7	2.1	2.4	1.6	4.7	4.6	4.8
Ranunculus ensyii	1.4	2.3	1.9	1.9	1.1	1.4	1.4	1.2	1.3
Raoulia grandiflora	1.4	1.3	1.3	2.5	0.7	1.4	2.2	1.7	2.0
Viola cunninghamii	1.1	0.9	1.0	1.9	0.7	1.2	1.4	0.9	1.1
Wahlembergia albomarginata	3.3	5.4	4.4	0.3	1.1	0.8	2.2	5.2	4.3
Fern spp	2.9	1.3	1.7	7.0	3.3	4.8	1.1	1.3	1.3
Polytrichum juniperinum	5.5	2.9	3.8	3.6	1.6	2.4	5.6	4.0	4.7
Allflower parts	17.1	16.9	16.5	16.3	11.6	13.6	17.8	14.1	15.9
TOTAL	80.8	80.0	77.2	85.3	82.5	82.7	78.7	85.7	85.8

contribution of selected plant species to the total diet of adults of grasshopper species from all the plots. The twentythree plant species or genera included, together with ingestion of flowers, constituted some 80% of the total intake of the grasshoppers in each class. As the sum totals for each grasshopper species and sex were very similar, this indicated a similarity in the overall choice between the most important plants.

Chi square analysis of the individual contributions of plants to the diet of grasshopper species showed that differences in selectivity were not significantly different. However some of the differences in intake between species appeared to be quite large. For instance P.nitidus exhibited a much higher intake of Celmisia lyallii, fern species, Aciphylla monroi and Gentiana corymbifera than did the other two grasshopper species. With the notable exception of G.corymbifera it seems that P.nitidus is more tolerant of the less succulent species.

S.australis for which the general range of occupation appeared to be similar to that of P.nitidus, appeared to show the greatest preference for the succulent, more generally favoured species. It had a higher intake of Celmisia spectabilis and C.viscosa in comparison with C.lyallii, and of the grasshopper species showed greatest preference for the most succulent grasses, Poa mackayii and Lachnagrostis forsteri, and the lowest intake of Chionochloa pallens. However a strong pattern in food preferences of S.australis also appeared

in relation to the growth form of the plants. A high preferability was shown for very low growing plants, evidenced by the highest intake of Anisotome aromatica, Pratia angulata, Raoulia grandiflora and Polytrichum juniperinum. This may also partly account for the low incidence of Chionochloa pallens and Celmisia lyallii, as well as the more erect shrubby species, for example the Hebe species. This feeding pattern may be the result of, or lend explanation to the observed preponderance of S.australis on more open sites within habitats compared to P.nitidus. Extrapolating still further, the reason for the mottled cryptic colouring patterns rather than the striped tonings of Paprides may be to tone with the more open type of background, rather than that of tall tussock vegetation.

B.nivalis showed greatest intake among the grasshoppers of the shrubby plants such as Hebe and Coprosma species, and for the Epilobium species. These differences in feeding intake may in part indicate differences in the availability of, rather than in real preferences for the plants. However B.nivalis appeared to have some more specialized ability for locating very sparse scree plants over the other grasshoppers. Grasshoppers of Brachaspis and Paprides were collected from open scree in the late evening near plot C5S. The crops of B.nivalis were full, containing species found on the scree, while those of the P.nitidus individuals were either empty, or contained a few fragments of plants contained in vegetation adjacent to the scree.

Ingestion by Sexes

Similarly wide fluctuations were noted to occur in the relative contribution of plant species to the diet of different sexes of the same species, as between the grasshoppers species themselves (Table 12). For instance the Celmisia species, Anisotome aromatica and Wahlembergia albomarginata were among those which appeared to be preferred by females of the species, and Epilobium species, Polytrichum juniperinum, Viola cunninghamii and flowers were taken in greater quantities by males. Chi-square analysis for differences in intake between sexes were not significant, and no patterns in selection were discernable.

Hansen and Ueckert (1970) found that the index of similarity of diets was relatively low for males and female grasshoppers of the same species in Colorado. Further to this, adult males ate fewer plant species than did adult females of the respective grasshopper species. This is consistent with findings in the present study, as evidenced by the ingestion rates determined for grasshoppers in Table 8. Differences were sufficient to suggest to Hansen and Ueckert (1970) that adult male and female grasshoppers probably behaved as two different populations, an opinion further exemplified by the consistent differences in size and rate of metabolism between sexes.

Ingestion Ranking

In an attempt to further ascertain the reality of

differences in selectivity between grasshopper species, food was examined on the basis of rank of ingestion for the grasshopper species, both for overall diet and by plots. In Table 13 the six most important plants in the diet of each grasshopper species and sex (from Table 12) were listed, in addition to flower ingestion which formed the most common component of diet for all grasshopper classes. It was revealed that for each species of grasshopper, the top three plants ingested (excluding flower ingestion) were all included within the top six as ingested by the two sexes. These top three plants contributed together, to some 20% of the total food selections by individual grasshopper species, and all contributed to greater than 5% of the overall diet, with the exception of Epilobium species for B.nivalis (49%). Furthermore Poa colensoi was the only plant species in the top three rankings that was shared by the grasshopper species, and this was shared by all three species. The entire table included twelve plant groups apart from flowers, all of which were included in the top twelve rankings for the entire grasshopper diet determined from Table 9.

In Table 14, the three most commonly ingested plants were derived for each grasshopper species for each plot, from ingestion data in Appendix B. The plants were listed where the individual ingestion records included three or more occurrences for each plant. It was seen that a large number of plant species were included in these rankings. More importantly

TABLE 13

Ranked Food Preferences by Grasshopper Species (from All Plots)

Ingestion Ranking	1 - 7 Ranked Plant Categories [a,b]								
	B.nivalis			P.nitidus			S.australis		
	♂	♀	Combined	♂	♀	Combined	♂	♀	Combined
1.	Fl	Fl	Fl*	Fl	Fl	Fl*	Fl	Fl	Fl*
2.	HEspp	POco	POco*	Fern	CEly	CEly*	POco	ANar	ANar*
3.	POco	CEvi	HEspp*	GAde	POco	POco*	CEvi	POco	POco*
4.	EPspp	WAal	EPspp*	GEco	ANar	GAde*	POju	CEvi	CEvi*
5.	POju	ANar	WAal	CEly	ACmo	Fern	ANar	WAal	PRan
6.	COspp	EPspp	CEvi	POco	CEvi	ANar	PRan	PRan	POju
7.	GAde	HEspp	POju	LUspp	GAde	GEco	EPspp	LUspp	WAal

a data extracted from Table 12

b shorthand notation formed from first two letters of generic and specific names, given in full below

* plant ranked in both male and female for a given grasshopper species

___ divides plant categories contributing > 5% of total food selections.

Summary : 1-20 Ranked Plant Categories in overall Grasshopper Ingestion[c]

1.	Fl	Flowerparts	12.	HEspp	Hebe species
2.	POco	Poa colensoi	13.	PRan	Pratia angulata
3.	ANar	Anisotome aromatica	14.	EPspp	Epilobium species
4.	CEvi	Celmisia viscosa	15.	CEsp+	Celmisia spectabilis
5.	GAde	Gaultheria depressa		LAfo+	Lachnagrostis forsteri
6.	CEly	Celmisia lyallii	17.	DRde+	Drapetes dieffenbachii
7.	LUspp	Luzula species		RAen+	Ranunculus ensyii
8.	COspp	Coprosma species	19.	ACmo+	Aciphylla monroi
9.	POju	Polytrichum juniperinum	20.	POma+	Poa mackayi
10.	Fern	Fern species		GEco	Gentiana corymbifera
11.	WAal	Wahlenbergia albomarginata			

c data extracted from Table 9

\+ not ranked 1-7 for any grasshopper category in top section of table

TABLE 14

Plant Ingestion Rank by Grasshopper Species and Plot*

	C1V	C1S	C2V	C2S	C3S	C40	C5V	C5S	A1V	A10	A2V	A2V2	A20	A3S	A4V	A40	A50	A3R	TR
B.nivalis	-	GAde	-	POco	HEpi	HEpi	-	PLspp	POma	POco	-	-	DRpr	CEvi	-	CHcr	PRan	NOse	HEpi
	-	POco	-	WAal	EPspp	WAal	-	COpu	POco	RAan	-	-	POco	POco	-	ANar	NOse	HEch	POco
	-	POju	-	ANar	POco	LUru	-	ANar	POju	HEly	-	-	EPspp	DRde	-		POco	WAal	CEvi
		RUac			RAen	POju		WAal	PRan					ANar			CEly		
		ANar				POco			Blpe										
P.nitidus	GAde	GAde	GAde	COpu	HEpi	LUspp	GAde	GEco	Blpe	RAen	DRde	ANar	DRde	ACmo	CEly	POco	CEly	-	-
	POco	CEly	COpa	LUspp	SEco	SEco	ANar	GAde	POco	BLpe	CEsp	POco	ACmo	CEvi	CHcr	CEly	POco	-	-
	SEmi	ANar	CEsp	ANar	CEly	GAde	CEly	COpn	CEly	COspp	POco	DRde		GEco	ACmo	ACmo	NOse	-	-
				CEly	GAde		CEsp	LUru			ANar	LUspp							
												COspp							
S.australis	GAde	GAde	ANar	WAal	CEvi	CGsp	ANar	WAal	-	PLno	ANar	ANar	DRpr	POco	CEvi	CEvi	POju	-	-
	LAfo	WAal	LYfa	COspp	POco	WAal	CEvi	LAfo	-	RAen	POco	POco	CEla	CEvi	PRan	PRan	PRan	-	-
	POju	ANar	POco		LUspp	GAde	POju	LUspp	-	ANar	DRde	CEvi	ANar	POma	LAfo	LAfo	POco	-	-
		POco	WAal				PRan				CEla					WAal			
							LAfo				CEvi								

* Shorthand notation forward from first two letters of generic and specific names, given in full overleaf.

Table 14 (cont.)

Summary:

Plant species	No.plots in which ranked in top three				Plant species	No.plots in which ranked in top three			
	Bn	Pn	Sa	Total		Bn	Pn	Sa	Total
Poa colensoi	10	6	7	23	Lachnagrostis forsteri	-	-	5	5
Anisotome aromatica	5	5	7	19	Aciphylla monroi	-	4	-	4
Gaultheria depressa	1	7	3	11	Celmisia spectabilis	-	3	1	4
Celmisia viscosa	2	1	7	10	Gentiana corymbifera	-	4	-	4
Walhembergia albomarginata	4	-	6	10	Notodanthonia settifolia	2	1	-	3
Celmisia lyallii	1	8	-	9	Ranunculus ensyii	2	-	1	3
Luzula species	1	4	2	7	Dracophyllum pronum	1	-	1	2
Coprosma species	1	5	1	7	Epilobrium species	2	-	-	2
Hebe species	5	1	-	6	Celmisia laricifolia	-	-	2	2
Polytrichum juniperinum	3	-	3	6	Poa mackayi	1	-	1	2
Drapetes dieffenbachii	1	3	1	5	Geranium microphyllum	-	1	-	1
Pratia angulata	1	-	4	5	Pinus species	1	-	-	1
Blechnum penna-marina)	1	2	-	4	Rumex acetosella	1	-	-	1
Lycopodes fastigiatum)	-	-	1						

Bn = Brachaspis nivalis

Pn = Paprides nitidus

Sa = Sigaus australis

it was observed that within each plot, different grasshopper species frequently included different plants in the rankings, indicating a differing rate of selection of plants from the same vegetation. The table is summarised into a list of the plants in order of the total number of plots from which they gained a ranking in the grasshopper ingestion. This list was noted to approximate the rankings for overall diet selectivity from Table 13. In addition, the values shown for grasshopper species were seen to reflect the relative favourability of the plants for these grasshoppers determined in Table 12.

The examinations of ingestion rankings, together with other evidence in this Chapter was enough to suggest that some degree of specialized selectivity of diet did occur in grasshopper species. However it is not possible to conclude from the data the basis for such differences i.e. whether they occurred as a result of differing inherent food preferences, or as a result of other aspects of feeding behaviour, such as the method of feeding, or as a result of occupation of different zones within the habitats. A much more comprehensive study would be required to confirm the reality and basis of differential selectivity of food by the grasshopper species.

D - MISCELLANEOUS INGESTION DATA

Empty Crops

Grasshopper collection periods were designed to minimise the occurrence of empty crops in the analysis. Even so a small proportion of crops (1.6%), evenly distributed throughout the grasshopper species and sexes, were found to be empty.

TABLE 15

Occurrence of Empty Crops in Adult Grasshoppers

Species		Incidence of empty crops		
		Number	% total	
B.nivalis	male	5	2.8	
	female	1	0.5	
	combined			1.5
P.nitidus	male	4	1.5	
	female	3	1.0	
	combined			1.2
S.australis				
	male	4	2.9	
	female	4	1.7	
	combined			2.2
Total combined incidence		21		1.6

This occurrence was found to be largely associated with freshly moulted individuals, or some that appeared to be senescing. In females, the incidence of a few empty guts was attributable to females that were very gravid and appeared about to be

ovipositing. Some males which were captured in copula were found to have empty or near empty crops, though this did not occur in females, which continued normal feeding behaviour during this state. The quantities contained in the crops of grasshoppers that contained food varied greatly, from a few fragments to a tight full condition with several hundred fragments.

Ingestion of Arthropods

Some 6.5% of adult grasshoppers were found to contain arthropod parts, sometimes in considerable quantities. This incidence of insect ingestion occurred from all plots, although the distribution of insect consumption appeared to vary within grasshopper classes, as revealed in Table 16.

TABLE 16

Ingestion of Arthropods by Adult Grasshoppers

Species		% incidence of Arthropod ingestion	
B.nivalis	male	5.1	
	female	15.5	
	combined		10.8
P.nitidus	male	2.6	
	female	3.2	
	combined		2.9
S.australis	male	3.7	
	female	12.0	
	combined		8.9
Total combined ingestion			6.5

Males had a lower ingestion rate than females, and P.nitidus appeared to ingest insects at a much lower rate than did the other two species.

Insect fragments were consumed in quantities that precluded the accidental intake along with plant food material. Dipteran insects were the most commonly ingested species, but also included were Lepidoptera and other winged and non-winged forms. The role of insects in the diet is not known. Larger insects were probably dead or at least immobilised when contacted by grasshoppers and may be ingested upon opportune contact. It was not ascertained that any fragements resulted from cannabalism, or from the ingestion of exuviae after moulting.

Mulkern et al (1962) and Hansen and Ueckert (1970) also noted the consumption of arthropods by grasshoppers. With the exception of one species, these were consumed at a rate usually considerably less than 9 percent of grasshopper individuals.

As previously mentioned, the grasshoppers were also observed to consume a wide range of other material. Some of this appeared to be accidental e.g. sand particles which were often found in conjunction with lichen eaten off rocks, and fungi which occasionally penetrated leaf tissues. However the observations indicated that the grasshoppers tended to be opportune feeders of somewhat omnivorous character. Restriction to a virtually phytophagous diet appeared, in some degree at least, to be by reason of availability only.

E - FOOD SELECTION BY JUVENILE GRASSHOPPERS

Host range

The very limited number of juvenile individuals examined precluded a detailed analysis of the feeding habits, although it appeared that in most respects the feeding behaviour was identical to that of adult grasshoppers. This was in contrast to the expectation expressed by Clarke (1948) that young instars would be restricted by a more delicate feeding apparatus to a range of the more succulent foods taken by adults. In the present study there was no indication of any restriction to that of the adult host range and juveniles of all stages were found to ingest plants in all of the favourability classes found for adults. However diversity in diet would in all probability be more restricted than that of adults, reflecting the much reduced mobility of juvenile individuals, particularly the earlier instars.

Ingestion Rate

The ingestion rate was calculated for 5th and 6th, and 1 - 4 instar groups, (Table 17). The ingestion rate was found to be similar in the two groups, with a range between 1.4 - 2.7. In each case the means were 1.9. Since only crops and not hindguts were analysed for the juveniles, these figures suggest that the feeding patterns were very similar to adults in the number of plant species fed upon at each meal.

TABLE 17

Features of Ingestion by Juvenile Grasshoppers

Plot	C1V	C1S	C2V	C2S	C3S	C4C	C5V	C5S	A1V	A1O	A2V	A2V2	A2O	A3S	A4V	A4O	A5O	TR	A3R	Total	Mean
INGESTION RATE																					
5 - 6 Instars																					
No.grasshoppers	8	14	6	14	9	11	7	-	9	4	23	17	19	6	4	13	-	17	3	184	
No.plant species consumed	17	29	11	20	18	21	12	-	14	8	42	32	39	9	7	19	-	37	7	351	
Ingestion rate	2.1	2.1	1.8	1.4	2.0	1.9	1.7	-	1.6	2.0	1.8	1.9	2.1	1.5	1.8	1.5	-	2.2	2.3		1.9
1 - 4 Instars																					
No.grasshoppers	6	21	10	-	10									3	-	8				58	
No.plant species consumed	16	40	16	-	17									4	-	17				110	
Ingestion Rate	2.7	1.9	1.6	-	1.7									1.3	-	2.1					1.9
EMPTY CROPS AND ARTHROPOD INGESTION																					
All Juvenile Instars																					
Empty crops (number)	3	2	2	-	4	1	1	-	1	-	-	1	5	-	-	3	-	-	-	23	9.7
Insect fragments (no.crops)	2	2	-	3	2	1	-	-	2	-	3	-	2	-	1	-	-	1	-	19	8.0

Empty Crops

These were found to occur in some 9.7% of all juvenile grasshoppers (Table 17), which was much higher than the adult rate of 1.6%. Empty crops were usually associated with freshly moulted grasshoppers.

Ingestion of Insects

Insects were recovered from 8.0% of juvenile individuals compared with an overall rate of 6.5% in adults. These findings contrasted slightly with the observation of Mulkern et al (1962) to the effect that the ingestion of such "extraneous" material increased in later instars.

F - SEASONALITY IN FOOD SELECTION

Because of the small total amount of feeding on each plant species by grasshoppers, an extensive analysis of ingestion in relation to the major sampling periods was not practical. However Table 18 the ingestion by time period of grasshopper sampling, are included for the ingestion of flower parts, fruit of Gaultheria depressa, and for Poa colensoi. The frequency values express grasshopper frequency, or the percentage incidence of the plants in grasshoppers.

Flowers proved to be extremely favourable to all species and formed the most commonly ingested component of the grasshopper

diet. It was noted that the ingestion of flowers showed a considerable seasonal influence. Consumption began with the onset of flowering sometime after the December collection and reached a peak in January before again declining by March. A difference in the intake of flowerparts between the successive January grasshopper samples reflected the increased availability of flowers in the 1969 season.

Fruit of G.depressa were apparently not consumed until maturation of the berries sometime after the January sampling.

The consumption of P.colensoi was revealed to decline markedly after the early part of the summer. This marked reduction probably did not reflect a decline in the favourability of P.colensoi as the season progressed, but rather the increased availability of the more favourable succulent species which appear annually, and especially the availability of flowers.

It is quite evident that grasshopper food consumption is greatly influenced by the seasonal availability of favourable food, and that studies of grasshopper diet must necessarily take this aspect into consideration, especially when attempting to assess total seasonal grasshopper damage to the vegetation.

Mulkern et al (1962) noted changes in diet of grasshoppers during the course of development. Seasonal changes in diet were observed by Uebekert (1968) to occur during the adult instar, which were attributed to seasonal changes relating to the favourability, nutritional quality and availability of food plants, and/or to

changing nutritional needs of grasshoppers. The seasonal changes were such that in some cases there was greater similarity between diets of different grasshopper species sampled on the same date than those of a single species sampled at different times in a season.

TABLE 18

Seasonal Influence on Feed Selection

	C1V	C1S	C2V	C2S	C3S	C4O	C5V	C5S	A1V	A1O	A2V	A2V2	A2S	A3S	A4V	A4O	A5O
Flowerparts. December 1969																	
Occurrence (No.of crops)	0	0	0	0	0	0	0	0	1	-	0	-	2	0	0	0	2
No.grasshoppers analysed	16	33	12	13	30	19	14	13	67	-	71	-	30	44	25	9	46
late January 1969																	
Occurence	11	19	11	8	30	23	18	12	16	19	14	7	20	30	28	22	23
No.grasshoppers	26	29	19	24	54	41	27	28	22	37	28	30	25	45	32	34	71
% Occurence	42	66	58	33	56	56	67	43	73	51	50	23	80	70	88	65	32
March 1969																	
Occurence	7	3	8	7	9	17	13	12	-	-	10	-	6	9	7	-	-
No.grasshoppers	16	40	40	21	25	37	44	32	-	-	29	-	32	33	39	-	-
½ Occurence	44	8	20	33	36	46	30	38	-	-	34	-	19	27	18	-	-
January 1970																	
Occurence	-	-	5	2	9	-	-	-	-	-	-	-	-	11	0	-	6
No.grasshoppers	-	-	28	18	28	-	-	-	-	-	-	-	-	30	11	-	37
% Occurence	-	-	18	11	32	-	-	-	-	-	-	-	-	37	0	-	16
Fruit of Gaultheria depressa																	
% Occurence " " Dec.'69	0	0	0	0	0	0	0	0	0	-	0	-	0	0	0	0	0
" " Jan.'69	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
" " Mar.'69	25	48	15	19	4	43	7	19	-	-	0	-	2	0	0	-	-
" " Jan.'70	-	-	0	5	0	-	-	-	-	-	-	-	-	0	0	-	0
Poa Colensoi																	
% Occurence " " Dec.'69	44	36	42	38	47	26	29	23	18	-	38	-	40	48	40	22	35
" " Jan.'69	31	21	5	33	0	5	15	11	18	19	21	30	12	7	3	15	30
" " Mar.'69	0	8	15	5	8	8	9	6	-	-	3	-	6	12	8	-	-
" " Jan.'70	-	-	18	17	4	-	-	-	-	-	-	-	-	10	0	-	8

CHAPTER 7

DISCUSSIONS AND CONCLUSIONS

DISCUSSION OF METHODS

Rather than the mere elucidation of feeding habits *per se*, the aim of determining the diet of the grasshopper species was to enable some preliminary insight into their potential role as feeders on the alpine vegetation, in order to facilitate the ultimate aim of determining their actual role, or pest status. This implied the necessity of relating the pattern of food selection by grasshoppers to the composition of the vegetation to determine the possible influence one upon the other. This requirement in turn necessitated an assessment of the vegetation as well as that of the diet of associated grasshoppers. It was concluded that the most conveniently obtained and readily marriageable data for the composition of vegetation and grasshopper diet was derived from determinations by point analysis of vegetation and epidermal analysis of gut contents respectively.

Siting of Plots

The plots selected for the collection of grasshoppers and analysis of vegetation were chosen to reflect typical sites of grasshopper occupation in the area. It was found that two species, Paprides nitidus and Sigaus australis were always associated in their general habitat with the dominant, tall tussock species of Chionochloa. The remaining two species, Brachaspis nivalis and Sigaus villosus were similarly dependent on scree debris, although the former was frequently sympatric with the vegetation-inhabiting species in a narrow band along scree verges or in very open tussock habitats that were interspersed with scree pavement. S.villosus occurred sparsely above altitudes of 5500' where it was sympatric with B.nivalis. At these altitudes the other two species were confined to small patches of vegetation remnants.

In all, 19 plots were included in the study. The major plant species of Chionochloa and Celmisia, and more important minor species generally occurred with a high degree of constancy between plots. However their contribution to total cover varied widely. The presence of many of the minor species was highly variable, variously reflecting aspects of altitude, moisture, density of dominant species, length of snow lie or solar radiation.

In a broader sense the plots were representative of the type of vegetation occupied by grasshoppers throughout the alpine areas, though more especially the drier areas east of the

main divide which are developed on a greywacke parent material. Therefore in a general sense, the results obtained of feeding selectivity might apply over the range in which grasshopper species may be an important factor in land stability.

Analysis of Vegetation

The advantages of point analysis over other practicable methods of vegetation assessment were associated with its rapidity, and because it enabled assessment of absolute rather than merely specific frequency of plant composition. Thus the importance of individual components as a contribution to total plant cover could be assessed.

The analysis of 500 points per plot enabled a good representation of the major components of the vegetation to be obtained, although clearly a much greater number of points would be necessary to produce low standard errors of sampling for minor species. However sampling of the magnitude required was not practical in the present study, where the aim was not to analyse the vegetation *per se* but to provide a basis for comparing the relative abundance of plant species on a plot basis, with their frequency of ingestion by grasshoppers.

To overcome the problems of point analysing tall tussock vegetation, a modified point frame was used. As far as possible the vegetation was measured as the vertical projection onto the ground in order to gain a consistent and representative picture of the relative availability of plants to grasshoppers. Only

the first hit on each species was recorded, and the analysis was performed under conditions producing minimal seasonal or climatic bias.

The raw data, expressed as percentage cover, were useful in adding quantitative information to the descriptive analysis of each plot. However in order to make plots comparative on the basis of availability of plants as potential food for grasshoppers, the relative frequencies of plants were determined on the basis of the total cover of vegetation only, without regard to the variable contribution of litter, scree, erosion pavement and rock surface in each plot. Furthermore, the results expressed on the basis of total plant species contacted during point analysis, not frequency on the basis of total contacts on any vegetation. This therefore took into account the layering of vegetation, which was developed to varying degrees in different plots. The vegetation frequency used to compare with grasshopper ingestion data thus represented the availability of plant species with respect to all other plants in the vegetation.

Analysis of Grasshopper Diet

Identification of gut contents by epidermal analysis of the fragments enabled the assemblage of a large amount of feeding data over a season since grasshopper specimens could be stored indefinitely. This freed favourable weather for field work, the grasshoppers collected being later analysed in the

laboratory. The results obtained furthermore, represented the *in situ* food ingestion of the grasshopper individuals from their respective plots at the time of collection.

Grasshoppers were collected over areas around each plot representative of that for which the vegetation analysis had been conducted. The grasshoppers were collected with the aim of providing a representative sample of the population on the plot, so that combined grasshopper intake could be usefully compared with the vegetation composition on a plot basis. However the degree of efficiency in obtaining a representative sample of grasshoppers by random collection is doubtful because of differences in elusiveness between grasshopper species and sex classes. Males are therefore probably underestimated to females for instance. However the later analysis of food selection revealed that as all the grasshoppers were of general feeding habits, the bias introduced from grasshopper sampling is probably inconsequential, in a qualitative sense.

Identification of gut contents depended upon the establishment of a reference collection of leaf epidermis surfaces. Where possible the section was made from the whole leaf, or else from a section midway along the lamina. Both upper and lower surfaces were prepared and mounted in a manner that enabled rapid comparison of the reference slide to fragments of any portion of the leaf recovered from grasshopper guts. This, together with a card index keying system formed the major means of identification of cuticle fragments.

The grasshopper crops provided the best source of food to examine. The contents of the hindgut were found to vary with the time from the last defecation, but contained at capacity the equivalent of two fecal pellets. This was several times smaller than the capacity of the crop. However the hindgut frequently contained fragments of different species in addition to those in the crop which might or might not have represented a different feeding period. Therefore, for a qualitative study of food selection such as the present, analysis of hindgut as well as foregut enabled an effective increase in information obtained from each grasshopper. Analysis of hindgut added little to the time required to analyse food for each grasshopper.

The fragments from each gut section could be examined on one microscope slide. Bleach was used to clear the fragments though staining was not found necessary. Where less than five fragments of a species were recovered from a grasshopper, the result was recorded, but not used in the analysis. This was to avoid plants whose presence may have been merely the result of test biting a plant, rather than its acceptance as food.

The tabulation of individual examinations on a card index system enabled comparison of results on bases of plot or time of collection, and species, age or sex classes of grasshopper. However because of the unanticipated generality of feeding habits revealed for all species, a detailed analysis of results from all of these categories was not possible because of inadequate

samples in some categories. In future studies of a similar nature, it would be prudent to examine larger numbers of grasshoppers from perhaps fewer collecting sites than the 19 utilised in this study. It was found that in order to gain a reasonably consistent representation of all but very minor plant species in the grasshoppers, on a qualitative basis, generally the analysis of about 100 grasshoppers would be required for each category.

Grasshopper gut contents may be analysed on both a qualitative (presence or absence) basis, or quantitatively by analysing the amounts of each food item present. In the latter case analysis could be with regard to the gravimetric, volumetric or numeric quantities of food in the gut. Such strictly quantitative studies of food consumption have been undertaken so far. In the case of grasshoppers studied by Mulkern et al (1962, 1964, 1969) most of the grasshoppers only contained single plant species. Their damage potential was therefore expressed on the basis of the frequency of plant consumption and the average crop weights. A quantitative analysis of the diet of multiple feeding grasshoppers would require determination of the relative quantities of each food item consumed.

The present study was of a qualitative nature. However the trends shown in feeding preferences were also expected to be of a similar nature on a quantitative basis, except that the real differences between favourable and unfavourable foods would

be even more accentuated. This was because a favourable species could be expected to be ingested more frequently when contacted than an unfavourable species, and in addition, more of it would probably be consumed for each feeding contact.

The methods of assessing and presentation of massed data were chosen to have most meaningful relationship with the study aims of defining the diet of the four species of grasshopper, and the relationship between grasshopper feeding and vegetation. Since it was impractical to record the food contents of every individual, the results were summarised on a plot basis.

The data was then converted to frequency values to enable comparison between samples of varying sizes. The frequency could either be a statement of the incidence of food in the gut on the basis of the total number of grasshoppers, or as the total number of food items ingested (i.e. food selections made) by the grasshoppers. As the present study was a qualitative investigation of food selection it was decided to use the latter method. This enabled the more meaningful comparison of ingestion between grasshopper classes, and between plots, since the number of food items recovered per grasshopper varied quite considerably both individually and between the class and plot categories. Furthermore since frequency values for both vegetation and grasshopper analyses represented absolute frequencies, pertaining only to plant species, the frequency estimates were directly inter- and intra- comparable, both within and between plots.

The laboratory analyses of gut contents were only able to determine what grasshoppers had ingested. It was essential to the full interpretation of these results therefore, to observe feeding behaviour of grasshoppers in the field to also determine how, when and where food was taken, and to what extent the sources of supply were visibly exploited. However the scope of such investigation was limited by the short duration of the summer period, and effective time that could be spent was further restricted to periods of optimal climatic conditions. The time required to gain each item of information on actual food selection restricted the use of direct observations as a means of diet determination when compared to gut analysis.

CONCLUSIONS ON GRASSHOPPER DIET

Field observations revealed that all four grasshopper species exhibited essentially similar feeding behaviour, which was in general typical of that described for other grasshopper species inhabiting range-type grassland situations. The grasshoppers were shown to be periodic daytime feeders, with feeding behaviour interspersed by long periods predominantly occupied in basking behaviour. The grasshoppers were not evident during cold conditions, or at night, when they occupied shelter positions generally in the bases of tall snow

tussocks, or under scree debris depending upon species.

Observations of feeding indicated that the location of food was largely on the basis of random searching, and that potential food was accepted or rejected principally on the basis of gustatory responses after contact had been made with mouthpart receptors. This inferred that the occurrence of food in grasshoppers was influenced by the interaction of two major factors; the abundance of plant species in the vegetation, and the relative favourability of plants to the grasshoppers principally with regard to chemical, but also morphological, composition.

When feeding, all grasshopper species exhibited the characteristics of multiple food selection, by visiting, and usually feeding on more than one plant before discontinuing feeding. They generally walked from plant to plant at random, testing each contact with antennae or palps, followed by test biting before either staying to feed for varying periods, or moving immediately to another plant. Epidermal analysis revealed that the extent of this behaviour varied widely with from one, up to eight, different plants recovered per grasshopper. The overall average was 2.6. Males appeared to have a lower rate of ingestion than females, and P.nitidus appeared to have a slightly lower ingestion rate than did other species. However the differences did not reach statistical significance when analysed. There appeared to be no great difference in this multiple feeding behaviour

in juvenile individuals.

These findings were in slight contrast to those of Mulkern et al (1962, 1964, 1969) for which in the majority of species investigated, one plant food was recovered. The significance of this feeding behaviour was concluded to be an adaptation having the advantageous effect of distributing feeding pressure more evenly. This reduced the possibility of the overexploitation of individual plants which, because of the harshness of the environment, are very slow growing and low producing. In such an environment the need for such adaptations resulting in conservation of food sources are in the long term more advantageous than the exploitation which occurs, and which is expedient, in the grasshopper populations of widely different environmental circumstances. This is discussed more fully later.

On the basis of host range, plant specificity index, and the proportion of consumption between monocotyledonous and dicotyledonous plant species all determined from epidermal analysis, it was concluded that the four grasshopper species were all of broadly similar, very general feeding habits. The nature of food consumed revealed that the major proportion of the diet was contributed by plant leaves of no particular taxonomical origin, though the high seasonal ingestion of flower parts, and low, but significant, incidence of arthropod remains suggested that they were opportunistic feeders.

The host range of all species was considered to be ubiquitous among the plants in their natural habitats. Therefore the host range was determined to a large extent by what was available in the vegetation rather than by inherent preferences of the grasshoppers themselves. However it was also shown that plant species were ingested in varying rates with respect to their abundance in the vegetation. This inferred that there was a degree of selectivity in the ingestion of food. It was concluded that the basis for this selectivity was largely the result of inherent preferences in the grasshoppers, rather than the result of the influence of different growth forms of plants, or the manner by which grasshoppers conducted their feeding behaviour. However such mechanisms may operate to produce the minor differences in food selection observed, between grasshopper species.

It was found that plant species divided into three rather distinct categories of relative favourability for the grasshopper population taken as a whole. The first group consisted of species which were ingested at a rate well below the level of their abundance in the vegetation. These species were few in number, but included two of the major components of the vegetation, the tall tussock species of Chionochloa and Celmisia lyallii, and also Dracophyllum pronum. These major species did not tend to be consumed in proportion to their abundance, but rather at a constant, low level which depended on their inherent favourability and the availability of more favourable species.

The middle group were consumed at a rate which was consistant overall, with their abundance in the vegetation. It was noted that these species tended to be of the same general conformation as the first group. Their ingestion response to abundance in this vegetation was also similar to that of the first group, though occurring at a higher level in proportion to its availability.

The third group were consumed at levels above that of their occurrence in the vegetation, some markedly so. Most of the species of this group formed very minor components of the vegetation. It could not be conceived, the extent to which this situation was the result of overexploitation of these species by grasshoppers. Some very minor species appeared to be under considerable selective pressure as evidenced by field damage caused by grasshopper feeding. For example species of Cardamine and Luzula rufa were seldom encountered in the field in undamaged condition late in the season. Hebe pinguifolia plants often exhibited extensive die back as a result of bud nipping, particularly on sites frequented by scree inhabiting species, such as the tope ridge site.

The overall pattern of food favourability appeared to be the result of selection largely on the basis of the succulence of plants. All those plants in the third category were of mesophytic growth type, compared to the other two groups which were of more xeric form. This was further exemplified by the marked favourability of flower and fruit parts as indicated by

their highly seasonal occurrence in grasshoppers. All of the categories contained monocotyledonous and dicotyledonous species indicating that selection was not on a major taxonomic basis. However lower plant taxons, of the cryptogams and mosses, were not found in the high favourability category.

The analysis of results for ingestion by juveniles was somewhat limiting, although it was concluded that the food habits were very little different from those of adults. Foods of all the favourability categories were recovered from juveniles. A slight reduction in diversity may be expected as a result of lesser mobility, particularly of younger instars, which reduces the chance of contact with minor plant species. The results also indicated a similarity to adults on the basis of the extent to which the multiple feeding habit was developed.

Although the criterion of succulence appeared to form the principal basis for favourability between plants, it could not be ascertained if this preference was a reflection of physical and/or chemcial properties affecting the selection. Cook and Harris (1968) found that nutritive values of range plants in Utah varied more greatly from one season to another than between species during any one period. Forman (1969) found that the caloric value of Bryophytes ranked among the lower caloric components of the ecosystem, with a mean value of about 4000 cal/gm dry weight. Bliss (1962) carried out similar analysis on plants of alpine tundra on Mt. Washington, New Hampshire. Shrub species were found to contain the highest

caloric content in the shoots, with an average of 5000 cal/gm ash free oven dry weight. Herbaceous species ranked next with an overall mean of 4600 cal/gm, mosses at 4400 cal/gm and lichens lowest at 4300 cal/gm. There was considerable overlap in the caloric values within these classes e.g. Polytrichum juniperinum, contained the highest moss caloric content at 4700 cal/gm, which was higher than that of many species in the highest category. The higher caloric content in the perennial shrubby species was attributed to the higher content of structural components. Both Bliss (1962) and Forman (1969) found that plants of alpine areas had significantly higher caloric values than their corresponding species in tropical and temperate regions, a factor attributed to higher lipid values. The lipid values were found to amount to between 2.7 and 4.5% of dry weight in evergreen species and 1.4 - 2.7% in herbaceous plants (Hadley and Bliss, 1964). These values generally increased over the season, a factor that was attributed to the efficiency of lipids as a storage product. However it could also have an influence on cold tolerance requirements in the plants. In contrast to caloric values, Hadley and Bliss (1964) found that protein values were higher in herbaceous species at 15 - 20% ash free oven dry weight, compared with 10 - 15% content in evergreen species. A decrease occurred in most species over the growing season. This was more marked in perennial species, old evergreen leaves containing 8 - 10% protein. It appeared therefore, that if the nutritional quality of food formed the

underlying basis for diet selectivity, then protein intake rather than caloric consumption might be more important. The high degree of favourability of flowerparts, and the commonality of insect ingestion (6.5% of all individuals) lends further support to the opinion that the more proteinaceous foods are keenly sought.

Brown (1937) studied the excretia of Melanoplus bivittatus fed on artificial diets and found that monosaccharides were utilised completely, whereas polysacchorides sugars and starches passed through the alimentary tract with practically no change. However protein was entirely absent from the excreta, which suggested that it forms a major nutrient substance extracted from food by grasshoppers.

Although all grasshoppers exhibited the same host range, evidence did appear for the existence of a broad statistical selectivity between plant species by the grasshopper species. P.nitidus appeared to be more tolerant of the less succulent species than did S.australis, with which it is largely sympatric. In S.australis slight emphasis appeared on the selection of more succulent species, especially those of very low growth habit. B.nivalis tended to exhibit slight specialization towards the selection of shrubby species. It is not known whether this selective specialization between species was on the basis of slight differences in behaviour when locating or partkaing of food, or as the result of inherent preferences in the species, or as a reflection of some degree of occupational specialization

within habitats. More intensive study is required to confirm the significance of intraspecific food selectivity, and the basis for its operation.

Implications of the Feeding Selectivity to Grasshoppers

The differences in feeding selection in the New Zealand grasshoppers were much less than those shown by Mulkern et al (1962, 1964) and Anderson and Wright (1952) for American rangeland grasshopper species. In contrast to the North American populations however, New Zealand populations represented only one subfamily, and many fewer species. The generally low degree of feeding specialization in New Zealand grasshoppers could imply, in accordance with Gaussian principles, that they have developed under conditions of low interspecific competition for food. Gaussos' law states that two species cannot continue to exist in direct competition for a limiting resource without diverging in their requirements for the resource, or the extinction of one species from the area. If so, this low interspecific competition might either have been the result of allopatry in former times, or by factors other than food limiting respective populations. Although sympatry in New Zealand grasshoppers occurs to the extent that they may share in the same feeding areas, this sympatry might not in fact occur at levels of distribution at which food selection most frequently takes place for each species. Such specialization may account for small

differences observed in food selection. However it seems more likely that partial specialization of feeding on such a basis, with each grasshopper species retaining general food habits represents the most efficient means of conserving the food resources of grasshoppers, and also retaining maximum adaptability of feeding.

Caplan (1966) attempted to show by means of differential feeding tests, that three sympatric species of Melanoplus grasshoppers were sufficiently distinctive to overcome food competition, and therefore not to infringe Gaussian principles. However in applying this competitive exclusion principle, it is necessary to establish a common resource as an object of competition i,e. that it is actually or potentially limiting. It may well have been that food was not a factor limiting to the populations. An under compensation for difference in grasshopper size of the species in the experimental design of Caplan (1966) resulted in biased ingestion data based on the quantitative consumption of leaves. Furthermore the conclusions made did not take into consideration the influence of relative abundance of plants on their relative ingestion rates in natural conditions, when interpreting the results obtained from differential feeding tests.

However a low degree of feeding specialization implies a condition of optimum availability of food to the grasshoppers and also optimal adaptability to changes in the vegetation. Mulkern et al (1962) found that those species with the widest

range of host plants utilized the greatest proportion of available food, and were the most common. The seven most common species were found to ingest food in the closest relation to its abundance and were therefore more adaptable to varying habitats. Those species with narrow host range utilized only a small proportion of available food and were limited in distribution.

With respect to the New Zealand grasshoppers, it was observed that the taxonomic composition of vegetation was more important in determining grasshopper distribution and abundance by virtue of its influence on the structure of vegetation, rather than its influence on food for grasshoppers. Thus the distribution of grasshoppers in no way corresponded with the geographical distribution of any particular food plants, but the vegetation inhabiting grasshoppers were closely associated with the presence of tall tussock upon which they are dependent for shelter. Greatest numbers appeared to be developed in habitats formed by an optimum combination of tall tussock plants, and open sunny sites for basking. Open sites often provided the best feeding situations, containing the small succulent plants (forb or grass). Patches of warm exposed ground were also required for egg laying.

The low degree of specialization of feeding has implications with the plant insect relations in terms of optimal exploitation of vegetation by insects. The very general nature of feeding among the New Zealand grasshoppers might reflect a

specialization in itself, evolved from the necessity for conservation of food sources. In general the endemic alpine plant species have a very low genetic growth capability (Molloy, 1967) which is probably an adaptation to the harsh environment of rigorous climate and poor soil fertility. The over-exploitation of individual plants must therefore be protected against since they have a much reduced ability to recover by or during the next season, compared with their lowland counterparts.

Monroe (1967) divided insect populations into two groups on the basis of the influence of populations on the future availability of a potentially limiting resource:-

(i) those species whose present numbers did not determine the quantity of the resource available in future generations

(ii) those species whose numbers can influence the future quantity of a limiting resource.

Insects of the first group were characterised by a high rate of natural increase when environmental circumstances were favourable, after which there was a decline until the next favourable season. Peak populations occurred when the available quantity of a given resource was most abundant. These insects have not evolved from the need to conserve resources since peak numbers either occurred at times which seldom caused depletion of the resource in succeeding generations, or where the influence of over-exploitation was

in any case negligible compared with other periodically restricting environmental influences, such as dry climate. Examples of this type of interaction are provided by grasshopper populations in hot arid areas. These have little influence over the future production of a predominantly annual type of vegetation controlled by moisture cycles. Survival of the population is therefore best provided for by the maximal use of the resource as available to produce the largest numbers of progeny. Plague numbers are seen to be terminated as the result of environmental reversals rather than social interactions in the populations. In these cases it is probably also advantageous that species develop specialization in feeding to ensure optimal utilization of food resources and reduce competition between species.

Populations in the second category tended to show characteristics which tend to conserve resources in order to reduce the danger of depletion for future generations. This situation is clearly evident in the New Zealand grasshopper populations. It was noted that the grasshopper populations did not appear to exhibit the wild fluctuations of those in more arid climates. This was advantageous to the grasshoppers since overexploited vegetation in any one year would be unlikely to recover in the next season, and was furthermore highly vulnerable to further depletion with the initiation of erosion. The general stability of populations is probably the result of several factors. The condition of

the vegetation is very much more constant than that of arid areas, as moisture is not a limiting factor, and the vegetation is predominantly perennial rather than annual. Secondly the grasshoppers with a multiseasonal life cycle, are equipped with a slow rate of natural increase and are therefore less readily able to respond to fluctuating environmental conditions. Since mechanisms which prevent overcrowding tended to enable maximum survival for succeeding generations if a resource may become limiting, Monroe (1966) considered the possibility of social factors operating to limit insect populations as occurs in higher animals. However it cannot be merely speculated that such factors operate to maintain consistant low levels in the endemic grasshopper populations.

A further means of reducing the dangerous exploitation of food supply is provided by the generality of food selection. This tends to distribute feeding damage as widely as possible, while also maintaining optimal availability. Feeding damage is even more widely dispersed by the pattern of multiple feeding, which appears to be developed to a higher degree in the endemic grasshoppers than those of less rigorous environments, and which has the effect of reducing the damage inflicted upon individual plants. It is probable that such behaviour is best served by, or even requires, a general host range, since the advantages of evolving feeding selectivity must be balanced with the increase in time and energy expended in the location of food (Miller, 1967).

Several advantages are also evident in the pattern of food selection observed for the grasshoppers, which may be a factor directly influencing, or indirectly resulting from the food selectivity. It was observed that the lowest pressure of feeding occurred on plants upon which the grasshoppers were dependent for shelter most notably the tall tussock species. The preference for succulent species, within a general feeding habit, meant that grasshoppers are able to make good utilization of the more favourable species as available, which were probably also nutritionally superior, whilst being able to fall back on the large reservoir of standing crop when not present. This implies that in the appropriate part of the season, and in favourable years for growth, feeding is concentrated on fast growing species and flowers, which can probably tolerate higher feeding pressures and thus reliev pressure on the slow growing evergreen perennials.

The generality of feeding behaviour of the four species studied appeared to reveal a continuation of the remarkable adaptation to the somewhat unique New Zealand alpine environment, already evidenced by their unusual life cycle pattern. It was observed that a multi-seasonal life cycle, plus an apparent hibernating, rather than diapausing response to cold temperature operating in later instars, enabled the grasshoppers to make optimal use of an environment of very erratic climatic fluctuations. The feeding pattern revealed for the grasshoppers was seen to facilitate such activity with the

optimum exploitation of the vegetation throughout the year.

Implications of Grasshopper Feeding on the Vegetation

One major implication for populations which are essentially conservers rather than exploiters of vegetation is that when the conditions under which they have evolved are permanently altered, so too the changes in insect population dynamics are also likely to be permanent. This infers the possibility that where changes in the vegetation are generally favourable, as appears to be the case in the New Zealand alpine grasslands for grasshoppers, the population permanently attains a new balance.

It has already been concluded that the alpine grasshoppers have evolved mechnisms for the efficient exploitation of vegetation under the conditions for which they have evolved. However, if grasshoppers occur in unfavourably high numbers under the conditions presently operating, then some unfavourable impact on the vegetation should be indicated. It is evident from preferred habitats of grasshoppers that greatest numbers are likely to occur on alpine vegetation which is less able to support them. The general trend is that unmodified stands, i.e. those approaching the climax condition, support low numbers of the vegetation-inhabiting species. As the stands become more open, greater numbers of these species are supported. There may also be a lesser degree of niche specialization or separation with a

consequently greater degree of sympatry at the feeding levels of distribution. This situation is accentuated when the vegetation becomes open enough after initiation of erosion, to support sympatric populations of scree species as well. At this stage there occurs exploitation of the food resources by the greatest number of species, all with similar, if not identical food habits.

If grasshoppers can be implicated in the deterioration of alpine grasslands, then some pattern in deterioration might be expected in relation to grasshopper food selection preferences. It was seen that, as a result of the general feeding habits of grasshoppers, no section of the vegetation is free from attack bygrasshoppers. The preference of grasshoppers for succulent species indicated that the generally minor species were most exposed to grasshopper attack. It might therefore be concluded that these species were most vulnerable if grasshopper populations were at unfavourably high levels. However it cannot be automatically concluded that they are more susceptable to deterioration since these often herbaceous species tend to have a higher growth rate and turnover of leaf production. They can therefore sustain a greater rate of removal at any time compared with the slow growing perennial species. Nordmeyer (1966) considered that the turnover rate of the grassland vegetation in the Craigieburn range was about 10%. This then infers that any damage to the leaves of the latter species would be cumulative over a period of up to, or exceeding ten years.

The role which minor species play in the seral succession and general vigour of the grassland community, is not known. However it is evident that a rich flora of minor species would relieve feeding pressure on major species, which largely contribute to soil stability.

One major implication of the preference for succulent plants is vulnerability of seedlings to grasshopper attack. Seedlings are both highly succulent, and occur close to ground level at which grasshopper feeding is concentrated. Furthermore seedlings would be very subject to mortality by a single feeding contact, especially by adult grasshoppers. The extent of seedling ingestion could not be determined from the present study. However grasshoppers were observed to consume, and destroy, seedlings in the field. Hence the major impact of unfavourably high grasshopper numbers could be the long term deterioration of the vegetation as a result of the prevention of regeneration in much the same manner as deer have affected beech forest vegetation.

The above conclusions imply that for the New Zealand alpine grassland situation, once the natural balance between the grasshoppers and vegetation has been upset as appears to have occurred, principally by fire, the grasshopper populations are potentially able to aggravate and perpetuate a downward trend in vegetation condition. This results from the adaptability of feeding by grasshoppers, which means that grasshoppers are able to move progressively from favourable to

unfavourable species as they disappear from the vegetation. The tendency for grasshopper numbers to increase as vegetation thins, together with more pronounced sympatry of species, increases feeding pressure and increases the potential for prevention of regeneration by seeding. This infers that bare patches are increasingly exposed to erosive forces probably to a stage beyond which the downward trend in vegetation condition is not readily reversible.

The reality of the role of grasshoppers in deterioration according to such an hypothesis should be open to test by examination of progressively deteriorating vegetation. It would be expected that in the initial stages as climax tussock is opened, an increase would occur in the low growing minor forb species due to better light conditions. However once erosion is initiated, a reduction in the availability of these more favoured species would occur, with the major forb components being replaced by the more grasshopper-resistant species e.g. Dracophyllum or Celmisia species, or by those which survive by means of high rate of reproduction and/or production e.g. Anisotome aromatica, Wahlembergia albomarginata. Such a pattern is in evidence. Shady areas, with low grasshopper numbers, are floristically richer than other areas, with the increase in species numbers tending to be contributed by the forb species, which are highly favourable to grasshoppers. A similar increase in floristic abundance seems to occur in the wetter alpine vegetation west of the main divide which also

enjoys lower grasshopper population densities. Deteriorated stands in the present study e.g. A3, 4 and 5 indicate that plants which are unfavourable to grasshoppers tend to be the last to disappear from the vegetation.

These effects do not necessarily implicate grasshoppers directly as a cause, since many other factors also contribute to such situations. However the events do not contradict the hypothesised role of grasshoppers in producing unfavourable influences on the vegetation.

SUMMARY

Insects have only recently been implicated in the deterioration of New Zealand alpine grassland vegetation. Among the most prominent of these insects are alpine grasshoppers.

As a preliminary to eventually defining the impact of alpine grasshoppers on the vegetation, a study of their dietary habits was instigated.

The study included a determination of the four species Brachaspis nivalis, Paprides nitidus, sigaus australis and sigaus villosus which were found within a study area located in the Broken River Catchment, Craigieburn Range, Canterbury.

Grasshopper diets were investigated with respect to the availability of food plants in plots from which the grasshoppers were collected. Diet determination was based principally on the epidermal analysis of grasshopper gut contents, while an assessment of the vegetation was conducted using the point analysis technique.

It was found that the four grasshopper species exhibited similar general feeding habits and food selectivity. The plant host range for all species appeared to include all plants available to them. However the grasshoppers tended to show a

preference for succulent plants, regardless of major taxonomic groupings. Such succulent monocotyledonous and dicotyledonous plants were consumed at a frequency level greater than that of their corresponding abundance in the vegetation. On a species basis these plants tended to be minor constituents of the vegetation. Flowers, when available, were a very highly favoured food by all grasshopper species.

Among plants which were in the lower favourability categories of grasshopper ingestion, many formed major components of vegetation composition. The least favoured of these food plants for all species were the large snow tussock (Chionochloa) species, which formed the dominant cover in the vegetation, and upon which grasshoppers seemed to be dependent for shelter.

Within the very broad host ranges, some differences in food selectivity were observed on the basis of ingestion frequencies between grasshopper species. Similar differences were also observed to occur between adult male and female grasshoppers of the same species. Juvenile grassshoppers appeared to exhibit similar general feeding behaviour to their corresponding adults.

All grasshopper species exhibited the behaviour of multiple feeding, in which individuals tended to consume food from more than one plant during any feeding period. This habit was developed to a greater degree in adult females compared to adult male grasshoppers, and to a lesser degree in Paprides

nitidus compared with the remaining species.

Marked seasonality occurred in the selection of food by grasshoppers. This appeared to be related to the availability of more highly favoured food types, particularly the presence of flowers. However it may also be related to seasonal changes in preference for certain plants as a result of changing chemical composition of the plants, or changing requirements of grasshoppers.

It was apparent that factors of grasshopper species and sex, and seasonality, must be considered in future studies on grasshopper diet, or in assessing damage caused by grasshopper populations.

It was concluded that the feeding habits exhibited by the grasshoppers showed and adaptation for the optimal utilization of the pristine vegetation, which under the rigorous environmental conditions, is characterised by low annual net production. Broad feeding habits of grasshoppers, and a multiple feeding habit tend to distribute feeding pressure, whilst maintaining greatest adaptability of grasshoppers to utilize food sources as available.

Where grasshopper populations assume unfavourably high numbers, as appears to be a case in some more open situations in the present vegetation, then an unfavourable impact would first be expected on the succulent minor species. A longer term depletion of the vegetation, as a result of impaired regeneration from seedlings would also be expected, in a

similar manner to the well documented depletion of forests by deer populations.

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APPENDIX A.

Floristic List of Plant Species Observed From All Plot Areas in the study area, Craigieburn Range.

CRYPTOGAMS

LICHENS (unidentified)

MUSCI

Polytrichum juniperinum Hedw.

Others not identified.

PHANEROGAMS

PTERIDOPHYTA

LYCOPODIALES

Lycopodium australianum (Herter) Allan

L. fastigiatum R. Br.

BLECHNACEAE

Blechnum penna - marina Kuhn

HYMENOPHYLLACEAE

Hymenophyllum villosum Col.

DRYOPTERIDACEAE

Polystichum cytostegia Armst.

SPERMATOPHYTA

GYMNOSPERMAE

Podocarpus nivalis Hook.

DICOTYLEDONAE

RANUNCULACEAE

Ranunculus ensyii T. Kirk

R. haastii Hook. f.

R. insignis Hook. f.

R. sericiophyllus Hook. f.

CRUCIFERAE

Cheesemania ensyii (Cheesem.) O.E. Schultz

Notothlaspi australe Hook. f.

N. rosulatum Hook. f.

Cardamine bilobata Kirk

C. debilis Banks and D.C.

VIOLACEAE

Viola cunninghamii Hook. f.

CARYOPHYLLACEAE

Colobanthus acicularis Hook. f.

Stellaria gracilenta Hook. f.

S. roughii Hook. f.

POLYGONACEAE

Muehlenbeckia axillaris Walp.

GERANEACEAE

Geranium microphyllum Hook. f.

ONAGRACEAE

Epilobium chloraefolium Haussk.

E. crassum Hook. f.

E. perplexum Kirk

E. pycnostachyum Haussk.

E. rubro - marginatum Cock.

THYMELAEACEAE

Drapetes dieffenbachii Hook.

Pimelea prostrata (J.R. & S. Forst) Willd.

PITTOSPORACEAE

Pittosporum crassicaule Laing and Gourlay

ROSACEAE

Acaena saccaticupula Bitter

A. inermis Hook. f.

Genm parviflorum Smith

UMBELLIFERAE

Hydrocotyle novae - Zealandiae D.C.

Schizeilema haastii (Hook. f.) Domin. (s.l.)

S. hydrocotyloides Domin.

S. roughii Hook. F. Domin

Oreomyrrhis colensoi Hook.f.

Aciphylla monroi Hook. f.

A. squarrossa

Anisotome aromatica Hook. f. (s.l.)

var. aromatica Hook. f.

var. dissecta Allan

A. carnosula (Hook. f.) Ckn. & Laing

A. filifolia Cock. & R.M.

ERICACEAE

Gaultheria crassa Allan

G. depressa Hook. f.

EPACRIDACERA

Cyathodes colensoi Hook. f.

C. fraseri (A.Cunn) Allan

C. pumila Hook. f.

Dracophyllum pronum Oliv.

D. uniflorum Hook. f.

MYRSINACEAE

Myrsine nummularia Hook. f.

RUBIACEAE

Coprosma cheesemanii Oliver.

C. petriei Cheesem.

C. pseudocuneata W.R.B. Oliver

C. pumila Hook. f.

Galium perpusillum (Hook.f.) Allan

COMPOSITAE

Brachycome sinclairii Hook.f.

Celmisia discolor Hook. f.

C. Dubia cheesem.

C. du - rietzii Cock & Allan

C. gracilenta Hook. f.

C. lyallii Hook. f.

C. laricifolia Hook. f.

C. spectabilis Hook. f.

C. sessiliflora Hook. f.

C. traversii Hook. f.

C. viscosa Hook. f.

Haastia sinclairii Hook. f.

Cotula pyrethrifolia Hook. f.

C. atrata Hook. f.

C. atrata var. dendyi Ckn. ex Cheesem.

Abrotanella caespotosa Petrie ex kirk

Gnathalium traversii Hook. f.

Raoulia grandiflora Hook. f.

R. bryoides Hook. f.

R. subsericea Hook. f.

Raoulia hybrids

Leucogenes grandiceps Beauv.

Helichrysum bellidioides Willd.

Craspedia lanata Hook.f.
Senecio Lagopus Raoul
S. lyallii Hook. f.
S. scorzoneroides Hook.f.
Taraxicum magellanicum Comm.

GENTIANACEAE

Gentiana corymbifera T.Kirk

PLANTAGINACEAE

Plantago novae - zealandiae L.B Moore

CAMPANULACEAE

Wahlembergia albomarginata Hook.

LOBELIACEAE

Pratia angulata Hook.f.
Lobelia roughii Hook. f.

STYLIDACEAE

Phyllachne colensoi (Hook.f.) Berggr.
Forstera tenella Hook. f.

BORAGINACEAE

Myosotis traversii Hook.f.
M. macranthra Benth. and Hook. f.

SCROPHULARIACEAE

Ourisia caespotosa Hook.f.
O. sessilifolia Hook. f.
Euphrasia petriei M.B. Ashwin
E. zealandica Wettst.
Pygmea pulvinaris Hook.f.
Hebe cheesemanii (Buch.) Cock. & Allan
H. epacridea (Hook.f.) Cock.
H. lycopodiodes (Hook.f.) Cock. & Allan
H. odora (Hook.f.) Cock.
H. pinguifolia (Hook.f.) Cock. & Allan

EXOTIC DICOTYLEDONAE

CARYOPHYLLACEAE

Cerastium vulgatum L.

POLYGONACEAE

Rumex acetosella L.

COMPOSITAE

Hieracium lachenalii L.

EXOTIC GYMNOSPERMAE

Pinus contorta
P. mugo

EXOTIC MONOCOTYLEDONAE

GRAMINEAE

Anthoxanthum odoratum L.
Festuca rubra
Holcus lanatus L.

MONOCOTYLEDONAE

LILIACEAE

Astelia nervosa Hook. f.

CYPERACEAE

Schoenus pauciflorus Hook.f.
Uncinia caespotosa Boott.

JUNCACEAE

Luzula pumila Hook. f.
L. rufa Edgar
L. traversii Cheesem.
Rostkovia gracilis

Agropyrum ensyii

A. scabrum Beauv.

Agrostis dyeri Petrie

A. subtulata Hook. f.

Chionochloa crassiuscula (Kirk) Zotov

C. flavescens Zotov

C. macra Zotov

C. oreophyla (Petrie) Zotov

C. pallens Zotov

C. rigida (Raoul) Zotov

Deyuxia avenoides Buch.

Erythranthera pumila (Kirk) Zotov

Festuca novae - zealandiae Cock.

Hierochloe fraseri var. recurvata Hook. f.

Koelaria kurtzii (Hack.) Petrie (s.l.)

Lachnagrostis forsteri

Microlaena colensoi (Hook.f.) Zotov

Notodanthonia settifolia (Hook.f.) Zotov

Poa colensoi Hook. f.

P. mackayi

P. sclerophylla Berggr.

Trisetum youngii Hook. f.

A P P E N D I X B.

DETAILS OF GRASSHOPPER INGESTION BY PLOTS.

The following tables list, for each plot, the numbers of grasshoppers within grasshopper categories, from which each food item was recovered. The grasshopper categories include adult male, adult female, and aggregated juvenile classes for each species sampled from plots, as well as the species totals and overall plot totals.

The total numbers of plant species ingested in each grasshopper category are also recorded, together with the average number of different plants found per grasshopper, where more than ten grasshoppers were analysed in any category.

Ingestion of each plant species was converted to percentage frequency of all plant categories consumed by the sum total of grasshoppers on plots.

Bn = *Brachaspis nivalis* Pn = *Paprides nitidus*

Sa = *Sigaus australis* Sv = *Sigaus villosus*

(*Chionochloa pallens* includes *C. rigida* and *C. macra*)

Appendix B (Contd,) Plot C1V

	ADULT Male		ADULT Female		JUVENILE		TOTALS Species		Grand	INGESTION FREQUENCY %
	Pn	Sa	Pn	Sa	Pn	Sa	Pn	Sa		
NO. GRASSHOPPERS	16	6	16	4	5	8	37	19	56	
INGESTION : MONOCOTS.										
Agropyrum scabrum				1				1	1	1
Chionochloa pallens	2		1	1			3	1	4	3
Hierochloa fraseri			1				1		1	1
Lachnagrostis forsteri	1	2	1		2		4	2	6	5
Luzula rufa	1			1		1	1	2	3	3
L. traversii	1		1				2		2	2
Poa colensoi	2	1	4		4	2	10	3	13	12
Uncinia angustifolia	1						1		1	1
DICOTS										
Anisotome aromatica	1		3			2	4	2	6	5
Celmisia laricifolia	1						1		1	1
C. lyallii			4		2		6		6	5
C. viscosa			1				1		1	1
Coprosma cheesemanii		1						1	1	1
Epilobium pedunculare		1						1	1	1
Gaultheria depressa	3	1	6		3	6	12	7	19	12
Geranium microphyllum	2	1	3		1		6	1	7	6
Geum uniflorum	1				1		2		2	2
Pratia angulata			1				1		1	1
Ranunculus ensyii	1						1		1	1
Raoulia grandiflora			1				1		1	1
Rumex acetosella	2			1		1	2	2	4	3
Schizoleima haastia				1				1	1	1
Taraxicum magellanism		1						1	1	1
Viola cunninghamii	1						1		1	1
Dicot. flower -unident.	6	3	3			3	6	6	15	13
- A. aromatica			2	1			2	1	3	3
fruit -G. depressa	1	1		1		1	1	3	4	3
MOSS & FERN										
Lycopodes fastigiatum			2				2		2	
Polytrichum juniperinum		2	1				1	2	3	
TOTAL INGESTION	27	14	35	7	13	16	75	37	112	
AV. INGESTION/GRASSHOPPER	2·0	2·2	2·3	1·3	2·3		2·1	1·0	2·0	
EMPTY CROPS			2	1	1		3	1	4	
ARTHROPOD INGESTION										
Lepidoptera			1				1		1	
Unidentified						1		1	1	

Appendix B (Contd.)

PLOT C1S

	ADULT Male			ADULT Female			JUVENILE			TOTALS Species			Grand	INGESTION FREQUENCY
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		%
NO. GRASSHOPPERS	9	13	5	26	9	7	18	8	9	53	30	21	104	
INGESTION : MONOCOT														
Agropyrum scabrum				2						2			2	1
Agrotis dyeri	1						1			2			2	1
Chinochloa pallens	1	2		2	1		1			4	3		7	7
Erythranthera pumila	1	1		1	1		1	1		3	3		6	3
Hierochloe fraseri					1						1		1	t
Lachnagrostis forsteri	1					1	1		1	2		2	4	2
Luzula spp.	2			4	1		2	1		8	2		10	4
Notodanthonia settifolia		1									1		1	t
Poa colensoi	2	1		3	1	3	6	2	3	11	4	6	20	9
P. mackayi						1						1	1	t
Trisetum youngii						1						1	1	t
Monocot flowerparts	2						2			4			4	2
DICOT														
Acaena inermis	1	2			1					1	3		4	2
Anisotome aromatica		1		4	3	3	2	4	2	6	8	5	19	8
Brachycome sinclairii	1									1			1	t
Cardamine debilis			1									1	1	t
Celmisia du-rietzii				1						1			1	t
C. lyalli		2	1	3	3		1			3	6	1	10	4
C. spectabilis				1						1			1	t
C. viscosa				1			2			3			3	1
Cotula spp.				2						2			2	1
Epilobium pedunculare			1	1						1		1	2	1
E. perplexum							1			1			1	t
E. rubrum	1			1			1		1	3		1	4	2
Gaultheria depressa	2	2		2	2	3	3	1	2	7	5	5	16	7
Geranium microphyllum					2			1			3		3	1
Hebe epicradea	1									1			1	t
H. lycopodioides							3			3			3	1
H. pinguifolia	1			3		1	1			5		1	6	3
Leucogenes grandiceps				1						1			1	t
Pimelea prostrata				1						1			1	t
Pratia angulata		1		2	2		2			4	3		7	3
Ranunculus ensyii		1		1		1				1	1	1	3	1
Rumex acetosella	1	2	1	3		1		1	2	4	3	4	11	5
Senecio scorzoneroides				1						1			1	t
Taraxicum magellanicum				2						2			2	1
Viola cunninghamii				2				1		2	1		3	1
Wahlenbergia albomarginata		1		3		3	1			4	1	3	8	4
Dicot flowerparts -unident.	5	1		4	2	3	4			13	3	3	19	8
-A. aromatica				2					1	2		1	3	1
fruit -G. depressa	2	2	3	6	1		2	1	2	10	4	5	19	8
MOSS & FERN														
Blechum penna-marina		1		1					1	1	1	1	3	1
Lycopodes fastigiatum		1									1		1	t
Polytrichum juniperinum	3	1		1		1	1			6	1	1	8	4
Unidentified moss	1						1	1		2	1		3	1
Lichen				1						1			1	t
TOTAL INGESTION	29	23	7	62	21	22	40	14	15	129	55	41	228	
AV. INGESTION/GRASSHOPPER	32	18		24	23					24	18	20	22	
EMPTY CROPS	1	1							2	1	1	2	4	
ARTHROPOD INGESTION														
Diptera				2						2			2	
Lepidoptera	1									1			1	
Unident.	1	1	4		2		1		1	6	1	3	10	

Appendix B (Contd.) PLOT C2V

	ADULT Male Bn	Male Pn	Male Sa	Female Pn	Female Sa	JUVENILE Pn	JUVENILE Sa	TOTALS Species Bn	TOTALS Species Pn	TOTALS Species Sa	Grand	INGESTION FREQUENCY %
NO. GRASSHOPPERS	1	18	9	26	29	13	3	1	57	41	99	
INGESTION : MONOCOT.												
Agrotis dyeri					2					2	2	1
Chionochloa pallens		1		3					4		4	1
Lachnagrostis forsteri		1	1	2	3		1		3	5	8	3
Luzula rufa		2	1	6	4	2	1		10	6	16	6
Microlaena colensoi				1					1		1	t
Poa colensoi		1		5	8	2	1	1	6	9	16	5
P. mackayi		1	1	1	2	1			3	3	6	2
Postkovia gracilis			1				1			2	2	1
Uncinia spp.				1					1		1	t
Monocot.flowerparts					1					1	1	t
DICOT.												
Anisotome aromatica		2		6	9	3			11	9	20	5
A. filiforme					1					1	1	t
Cardamine bilobata				1		1			2		2	1
Celisia lyalli		2	1	7	5				9	6	15	5
C. spectabilis		4		9	8	1			14	8	22	8
C. viscosa			1	3	5				3	6	9	3
Coprosma cheesemanii		1							1		1	t
C. pseudocuneata					1					1	1	t
C. pumila	1	4	3	9		2	1	1	15	4	20	7
Cotula pyrethrifolia					1					1	1	t
Drapetes dieffenbachii		1	4	1	1		1		2	6	8	3
Epilobium pedunculare				1	4				1	4	5	2
Euphrasia zealandica			1	1					1	1	2	1
Gaultheria depressa		1	8		7	5	2	1	17	5	23	8
Gentiana corymbifera			1		1				2		2	1
Geranium microphyllum					1				1		1	t
Hebe lycopodiodes					1				1		1	t
H. pinguifolia		3	1		2	1			4	3	7	2
Ourisia caespotosa				1	1				1	1	2	1
Plantago novae-zealandiae				3	2				3	2	5	2
Pratia angulata			1	1	1				1	2	3	1
Ranunculus ensyii		1		2	1	1			4	1	5	2
Raoulia grandiflora		1							1		1	t
Senecio lagopus					1					1	1	t
Wahlenbergia albomarginata			1	2	8	1			3	9	12	4
Viola cunninghamii		3							3		3	1
Dicot.flowerparts-unident.		6	3	4	5				10	8	18	6
-A. aromatica				3	4				3	4	7	2
fruit -G. depressa		1	1		2	1	1		2	4	6	2
Unidentified Dicot. leaves					1					1	1	t
MOSS & FERN												
Lycopodes fastigiatum		3	4	6	5		1		9	10	19	7
Polytrichum juniperinum			1		1					2	2	1
TOTAL INGESTION	3	49	26	90	94	18	8	3	153	127	282	
AV. INGESTION/GRASSHOPPER		27	29	35	32				27	34	29	
EMPTY CROPS						2			2			
ARTHROPOD INGESTION												
Diptera					1					1		
Unidentified				1	2				1	2		

Appendix B (Contd.) PLOT C3S

	ADULT Male			ADULT Female			JUVENILE			TOTALS Species			Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	9	26	16	12	24	19	5	3	11	26	53	46	125	
INGESTION : MONOCOT.														
Agropyrum scabrum							1		1	1		1	2	1
Chionochloa pallens		1					1			1	1		2	1
Lachnagrostis forsteri						5	1			1		5	6	2
Luzula spp.	1	4	2	1		3	1		2	3	4	7	14	4
Poa colensoi		3	2	4	1	6			1	4	4	9	17	5
P. mackayi			2	1		1			1	1		4	5	2
Uncinia caespotosa			1						1			2	2	1
Unidentified grass			1									1	1	t
Monocot. flowerparts						1						1	1	t
DICOT.														
Aciphylla monroi		1			4	1			2		5	3	8	2
Anisotome aromatica			2	1		2			2	1		6	7	2
A. filiforme					1						1		1	t
Carpha mine bilobata		3	1	1		1			1	1	3	3	7	2
Celmisia laricifolia		1		1	2					1	3		4	1
C. lyallii			6	1	5	1			1	1	11	2	14	4
C. spectabilis				2	3					2	3		5	2
C. viscosa	1	2	2	2	4	12			3	3	6	17	26	8
Coprosma pumila	1	1		1	1					2	2		4	1
Cotula pyrethrifolia						1						1	1	t
Drosophyllum pronum	1	1		2					1	3	1	1	5	2
Epilobium perplexum	1		1	3	2	1	1			5	2	2	9	3
E. rubrum	1					1			1	1		2	3	1
E. pycnostachyum	1			1						2			2	1
Gaultheria depressa		4	3	2	5	3				2	9	6	17	5
Gentiana corymbifera		5		1	6	1		1		1	12	1	14	4
Hebe lycopodiodes		3									3		3	1
H. pinguifolia	5	6	1		7					5	13	1	19	6
Pratia angulata		1	2	2	1	3	2			4	2	5	11	3
Ranunculus ensyii	2	2	2	2	5	1	1			5	7	3	15	5
Raoulia grandiflora			3	1	2	1			2	1	2	6	9	3
Plantago novae-zelandiae	1									1			1	t
Ourisia caepotosa	1									1			1	t
Senecio lagopus						1						1	1	t
S. scorzoneroides						1						1	1	t
Taraxicum magellanicum	1	1	3			1				1	1	4	6	2
Wahlembergia albomarginata		1	2			3					1	5	6	2
Viola cunninghamii		1	2			2			2		1	6	7	2
Dicot. flowerparts	4	9	8	5	9	6	2			11	18	14	43	13
A. aromatica flower	1			2		2	1			4		2	6	2
C. depressa fruit				1						1			1	t
Unidentified dicot leaf			2			1						3	3	1
MOSS & FERN														
Polytrichum juniperinum								1	1		1	1	2	1
Unidentified moss	2	1	1		1	2				2	2	3	7	2
TOTAL INGESTION	24	56	42	37	60	64	11	2	21	72	119	128	324	
AV. INGESTION/GRASSHOPPER	27	22	26	30	25	34				28	23	28	26	
EMPTY CROPS			1		2			1	2		3	3	6	
ARTHROPOD INGESTION														
Diptera				1	1	2				1	1	2	4	
Unidentified		1		1		2	2			3	1	2	6	

Appendix B (Contd.) PLOT C2S

	ADULT Male Bn	Pn	Sa	Female Bn	Pn	Sa	JUVENILE Bn	Pn	Sa	TOTAL Species Bn	Pn	Sa	Grand	INGESTION FREQUENCY %
NO. GRASSHOPPERS	18	4	3	20	9	12	11	1	2	49	14	17	80	
INGESTION : MONOCOT.														
Agropyrum scabrum				2						2			2	1
Chionochloa pallens	1			1						2			2	1
Lachnagostis forsteri				1		1				1		1	2	1
Luzula rufa	1		1	3	3	1	1			5	3	2	10	5
Poa colensoi	6			8	1	1	3			17	1	1	19	9
P. mackayi						2	1			1		2	3	1
Rytidosperma caespotosa	1									1			1	t
Monocot. flowerparts				1		1				1		1	2	t
DICOT.														
Aciphylla aromatica	3			5	3	1	1			9	3	1	13	6
Celmisia lyallii				4	3	2	1			5	3	2	10	5
C. spectabilis						2	1				2	1	3	1
C. viscosa				5		2				5		2	7	3
Coprosma cheesemanii		1		2	1		1			3	3		6	3
C. pseudocuneata				1		1				1		1	2	1
C. pumila	1	3	2	1	5	4	1			3	11	6	20	10
Dracophyllum pronum									2			2	2	1
Epilobium pedunculare	1			2			1			5			5	2
E. rubrum							1			1			1	t
Cotula pyrethrifolium						1						1	1	t
Gaultheria depressa	6				2					6	2		8	4
Gentiana corymbifera					1						1		1	t
Hebe epacridea	2			3						5			5	2
H. pinguifolia	2			1			1						4	2
Hieracium spp.				1						1			1	t
Veronica buchananii				1						1			1	t
Myrsine nummularia	2			2			1			5			5	2
Ourisia caespotosa						1						1	1	t
Plantago novae-zealandiae		1									1		1	t
Pratia angulata				1						1			1	t
Ranunculus ensyii				3						3			3	1
Rumex acetosella						1						1	1	t
Senecio lagopus				1		1				1		1	2	1
Wahlenbergia albomarginata	5			7		6			1	12		7	19	9
Viola cunninghamii					1	1					1	1	2	1
Dicot. flowerparts -Unident.	3		1	5	4	2	1			9	4	3	16	8
- A. aromatica				1		1				1		1	2	1
fruit -G. depressa	2			1	1	1	1			4	1	1	6	3
MOSS & FERN														
Blechnum penna-marina	1			1	1	2	1			3	1	2	6	3
Lycopodes fastigiatum	1				2			1		1	3		4	2
Polystichum cytostegia	1			3						4			4	2
Polytrichum juniperinum	1						1			2			2	1
Unidentified moss	1			2						3			3	1
TOTAL INGESTION	41	5	4	69	30	34	18	1	3	127	41	41	209	
AV. INGESTION/GRASSHOPPER	23			25	33	28				26	29	24	26	
EMPTY CROPS	1		1							1		1	2	
ARTHROPOD INGESTION														
Lepidoptera						1						1	1	
Unidentified				2			3			5			5	

Appendix B (Contd.) PLOT C40

	ADULT Male			ADULT Female			JUVENILE			TOTALS Species			Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	13	13	5	20	25	12	6	2	3	39	40	20	99	
INGESTION : MONOCOT.														
Chionochloa pallens				2			1			3			3	1
Deyuxia avenoides				1						1			1	t
Festuca novae-zealandiae				2	2					2	2		4	2
Luzula rufa		2		5	8		1			6	10		16	6
Poa colensoi	2	1		3	3	1		1		5	5	1	11	4
Uncinia caespotosa					1						1		1	t
Monocot. flowerparts		1		2		2	1			3	1	2	6	2
DICOT.														
Aciphylla monroi							1			1			1	t
Anisotome aromatica				3	1	1	1			4	1	1	6	2
Brachycome sinclairii								1			1		1	t
Celmisia gracilis					1						1		1	t
C. spectabilis	1			2	9	3		1		3	10	3	16	6
C. viscosa				1	1								2	1
Colobanthus acetabulum	1			1						2			2	1
Coprosma cheesemanii	2			1	1					3	1		4	2
Cyathodes fraseri			1		1						1	1	2	1
C. pumila				2						2			2	1
Dracophyllum pronum	2									2			2	1
Epilobium pycnostachyum	1									1			1	t
E. rubrum	1									1			1	t
Euphrazia zelandica				1						1			1	t
Gaultheria depressa		1		1	3	1				1	4	1	6	2
Gentiana corymbifera	1	3			3	1				1	6	1	8	3
Hoastia sinclairii				1	2					1	2		3	1
Hebe pinguifolia	10	1		4	6	2	3			12	7	2	26	10
Leucogenes grandiceps				5	1	2				5	1	2	8	3
Pimelea prostrata			1									1	1	t
Pratia angulata	1			2		2		1	1	3	1	3	7	3
Raoulia bryoides	1					1				1		1	2	1
R. subsericea	1				1					1	1		2	1
Rumex acetosella	2	2			3			1		3	5		8	3
Stellaria roughii				1		1				1		1	2	1
Wahlenbergia albomarginata	1			8	4	3							16	6
Viola cunninghamii					1	1					1	1	2	1
Dicot. flowerparts -uniden	5	5	3	9	8	8			2	14	13	13	40	16
fruit -G. depressa	1	3	2	3	5	2				4	8	4	16	6
Unidentified Dicot. leaves				1		1	1			2		1	3	1
TOTAL INGESTION	38	21	7	66	65	35				115	91	46	253	
AV. INGESTION/GRASSHOPPER	29	16		33	26	30				30	23	23	26	
EMPTY CROPS									1			1	1	
ARTHROPOD INGESTION														
Diptera	1			2						3			3	
Unidentified			1	3	2	1	1			4	2	2	8	

Appendix B (Contd.) PLOT C5V

	ADULT MALE		ADULT FEMALE		JUVENILE		TOTALS SPECIES		GRAND	INGESTION FREQUENCY
	Pn	Sa	Pn	Sa	Pn	Sa	Pn	Sa		%
NO. GRASSHOPPERS	19	9	21	30	6	1	46	40	86	
INGESTION : MONOCOT.										
Chionochloa pallens	1		2				3		3	1
Lachnagrostis forsteri	1	3	3	5			4	8	12	5
Luzula rufa	3	4		3	1		4	7	11	5
Poa colensoi	1	1	4	4	2		7	5	12	5
P. mackayi		2	2	5			2	7	9	4
Uncinia caespotusa	1		2	2			3	2	5	2
Monocot flowerparts		3						3	3	1
DICOT.										
Anisotome aromatica	1		6	14	1	1	8	15	23	10
A. filiforme	1			1			1	1	2	1
Cardamine debilis	3		1				4		4	2
Celmisia dubia				2				2	2	1
C. lyallii	3		3	4			6	4	10	4
C. spectabilis	1		5	1			6	1	7	3
C. viscosa	1			9			1	9	10	4
Coprosma cheesemanii			1				1		1	t
C. pumila				1				1	1	t
Dracophyllum pronum	1						1		1	t
Epilobium perplexum	1						1		1	t
E. rubrum	1						1		1	t
Euphrasia zelandica	3			5			3	5	8	3
Forstera tenella	1						1		1	t
Gaultheria depressa	6	2	7	5	1		14	7	21	9
Gentiana corymbifera	3		2		1	1	6	1	7	3
Geranium microphyllum	1						1		1	t
Hebe lycopodioides	1		3	2			4	2	6	3
H. pinguifolia	1						1		1	t
Pinus spp.	1						1		1	t
Pratia angulata	2	3	1	4		1	2	8	10	4
Ranunculus ensyii				1				1	1	t
Raoulia grandiflora				2				2	2	1
Senecio lagopus			2	2			2	2	4	2
Wahlenbergia albomarginata			1	4	1		2	4	6	3
Viola cunninghamii	1						1		1	t
Dicot flowerparts -unident.	8	3	2	5	1		11	8	19	8
-A. aromantica	1	2	6	3			7	5	12	5
fruit -G. depressa	1	1	1	1			2	2	4	2
MOSS & FERN										
Lycopodes fastigiatum	1						1		1	t
Polytrichum juniperinum	1	2	1	6	1		3	8	11	5
Unidentified moss			1				1		1	t
TOTAL INGESTION	52	36	56	93	9	3	109	120	229	
AV. INGESTION/GRASSHOPPER	27	29	27	31			24	30	27	
EMPTY CROPS					1		1		1	
ARTHROPOD INGESTION										
Diptera	1						1		1	
Unident.	1	1	1	1			2	2	4	

Appendix B (Contd.) PLOT C53

	ADULT Male			ADULT Female			JUVENILE	TOTALS Species				INGESTION FREQUENCY
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Bn	Pn	Sa	Grand	%
NO. GRASSHOPPERS	13	8	2	27	8	5	10	50	16	7		
INGESTION : MONOCOT.												
Chionochloa pallens				2			1	3			3	2
Lachnagrostis forsteri				1		2		1		2	3	2
Luzula rufa		2		1	2	2		1	4	2	7	4
Microlaena colensoi	1					1		1		1	2	1
Poa colensoi	1			4			1	6			6	3
P. mackayi				1				1			1	1
Unicinia caespotosa							1	1			1	1
Monocot. flowerparts				3				3			3	2
DICOT.												
Aciphylla monroi				1				1			1	1
Anistome aromatica		2		8				8	2		10	5
Celmisia du-rietzii	2							2			2	1
C. spectabilis	1			3		1		4		1	5	3
C. viscosa				3				3			3	2
Coprosma pumila	4	2		6	2	1	1	11	4	1	16	8
Cotula atrata	2			1				3			3	2
Epilobium crassum							1	1			1	1
E. rubrum							1	1			1	1
Euphrazzia zelandica	1	1		4	1	1		5	2	1	8	4
Gaultheria depressa	3	5						3	5		8	4
Gentiana corymbifera		2			3				5		5	3
Hebe epicrades	1			3				4			4	2
H. lycopodioides					1				1		1	1
H. pinguifolia	1	1			1			1	2		3	2
Pinus spp.	3			7			2	12			12	6
Pratia angulata				1				1			1	1
Ranunculus ensyii		2		1		1		1	2	1	4	2
R. haastii	1			2			2	5			5	3
Raoulia grandiflora				1				1			1	1
Senecio lagopus				2		1		2		1	3	2
Stellaria roughii	2			3				5			5	3
Wahlembergia albomarginata	2		1	5		4		7		5	12	6
Viola cunninghamii						1				1	1	1
Dicot. flowerparts Unident.	6	1	1	7	3		4	17	4	1	22	12
-A. aromatica						1				1	1	1
fruit G. depressa			1	3		2		3		3	6	3
Unident. dicot. leaves				1				1			1	1
MOSS & FERN												
Lycopodes fastigiatum					1					1	1	1
Polytrichum juniperinum	2						2	4			4	2
Unidentified moss			1							1	1	1
TOTAL INGESTION	33	15	4	74	14	18	16	130	30	22	189	
AV. INGESTION/GRASSHOPPER	25			27				26	19	31	26	
EMPTY CROPS	2	1					2	4	1		5	
ARTHROPOD INGESTION												
Diptera				1				1			1	
Unident.		1		3		1		3	1	1	5	

Appendix B (Contd.) PLOT A1V

	ADULT					JUVENILE		TOTALS			Grand	INGESTION FREQUENCY
	Male		Female					Species				
	Bn	Pn	Bn	Pn	Sa	Bn	Pn	Bn	Pn	Sa		%
NO. GRASSHOPPERS	13	25	22	19	4	3	6	38	50	4	92	
INGESTION : MONOCOT												
Agropyrum scabrum			2	2				2	2		4	2
Agrostis dyeri							1		1		1	t
Chionochloa pallens	3	1	1	2				4	3		7	3
Erythranthera pumilla	1	2		1				1	3		4	2
Festuca rubra	1							1			1	t
Lachnagrostis forsteri	2	2		2				2	4		6	3
Microlaena colensoi		1							1		1	t
Poa colensoi	3	4	6	3			1	9	8		17	8
P. mackayi	4	2	7	4	1	1		12	6	1	19	9
Uncinia caespotosa	1	1	1			1		3	1		4	2
Trisetum youngii		1	1	2				1	3		4	2
Monocot. flowerparts			1					1			1	t
Unidentified grass				2					2		2	1
DICOT.												
Acaena saccitacupula				2					2		2	1
Anisotome aromatica				1					1		1	t
A. filiforme		2							2		2	1
Cardamine debilis			1					1			1	t
Celmisia lyallii	2		1	7				3	7		10	5
Epilobium pedunculare	2							2			2	1
E. perplexum	2		5					7			7	3
E. rubrum	1		1					2			2	1
Geranium microphyllum				1					1		1	t
Gnathalium traversii					1					1	1	t
Hebe cheesemanii			1					1			1	t
H. epicradea			1					1			1	t
H. lycopodiodes	1			1			1	1	2		4	2
H. pinguifolia	2	4	1					3	4		7	3
Leucogenes grandiceps			1					1			1	t
Oreomyrrhis colensoi		1		2					3		3	1
Pratia angulata	1	1	3	2	1			4	3	1	8	4
Plantago novae-zealandiae					1					1	1	
Raoulia grandiflora	1		1		1	1	1	3		1	4	2
Rumex acetosella			1		1			1		1	2	1
Dicot.flowerpart -unident.	2	8	2	2		1		5	10		15	8
-A. aromatica				1					1			t
Unidentified dicot. leaves	1	1						1	1		2	1
MOSS & FERN												
Blechnum penna-marina	3	19	1	12	1		4	4	25	1	30	15
Polystichum cytostegia		1					1		1		1	t
P. juniperinum	2	1	2			1	2	5	3		8	4
Unidentified moss			1	1				1	1		2	1
TOTAL INGESTION	35	53	45	48	11	5	10	83	103	11	205	
AV. INGESTEION/GRASSHOPPER	27	21	20	25				21	21		22	
EMPTY CROPS			1				1	1	1		2	
ARTHROPOD INGESTION		1	6			1	1	7	2		9	

Appendix B (Contd.) PLOT A10

	ADULT Male			ADULT Female			JUVENILE			TOTALS Species			Grand	INGESTION FREQUENCY
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		%
NO. GRASSHOPPERS	3	6	4	8	6	6	2	2		13	14	10	37	
INGESTION : MONOCOTS.														
Agropyrum scabrum				1						1			1	1
Chionochloa pallens						1	2	2		2	2	1	5	4
Imbula rufa		1		2						2	1		3	3
Notodanthonia settifolia	1									1			1	1
Poa colensoi	1			3	1	1	1			5	1	1	7	6
P. mackayi			1					1			1	1	2	2
Rostkovia gracilis				1						1			1	1
DICOTS.														
Anisotome aromatica			1	1		2				1		3	4	3
Celmisia laricifolia						1						1	1	1
C. spectabalis					1	2					1	2	3	3
C. viscosa				1	1					1	1		2	2
Coprosma pseudocuneata	1	2		1	1					2	3		5	4
Cotula pyrethrifolia				1						1			1	1
Dracophyllum pronum			2									2		2
Epilobium pedunculare			2									2	2	2
E. perplexum					1						1		1	1
E. rubrum	1			1	1					2	1		3	3
Gaultheria depressa		1	1	1	1	1				1	2	2	5	4
Geranium microphyllum	1		1							1		1	2	2
Hebe lycopodiodes	1	1		2						3	1		4	3
H. linguifolia		1		1	1					1	2		3	3
Muehlenbeckia axillaris				1						1			1	1
Pittosporum crassicaule		1		1						1	1		2	2
Plantago novae-zealandiae			1	1		4				1		5	6	5
Pratia angulata					1						1		1	1
Ranunculus ensyii	1	3	2	4	2	2				5	5	4	14	12
Rumex acetosella								1		1			1	1
Senecio lagopus				1						1			1	1
Wahlenbergia albomarginata				1		2				1		2	3	3
Dicot. flowers -Unident.	3	1	2	5	2	3				8	3	5	16	14
- A. aromatica				1	1	1				1	1	1	3	3
Unidentified Dicot. leaves			1							1			1	1
MOSS & FERN														
Blechum penna-marina		2			2			1			5		5	4
Lycopodes fastigiatum		2				1					2	1	3	3
TOTAL INGESTION	10	15	14	34	16	21	4	4		46	35	34	115	
AV. INGESTION/GRASSHOPPER										35	25	34	31	
ARTHROPOD INGESTION				1		2				1		2	3	

Appendix B (Contd.) PLOT A2V

	ADULT Male			ADULT Female			JUVENILE			TOTAL Species			INGESTION Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	1	28	16	1	37	22		6	17	2	71	55	129	
INGESTION : MONOCOT.														
Chionochloa crassiuscula					3	1			1		3	2	5	1
C. pallens		1			1						2		2	1
Lachnagrostis fersteri			1						1			2	2	1
Luzula pumila					2						2		2	1
L. rufa		3	2		2	3			2		5	7	12	3
Microleana colensoi		1							1		1	1	2	1
Notodanthonia settifolia									1			1	1	t
Poa colensoi		5	5	1	7	12		3	2	1	15	19	35	10
P. mackayi					1	2					1	2	3	1
Uncinia caespotosa		3	2		4	1		1			8	3	11	3
Unidentified grass					1						1		1	t
DICOT.														
Aciphylla monroi		1			10	2			1		11	13	14	4
Anisotome aromatica		1	7		10	13		1	5		12	25	37	11
Celmisia dubia		1									1		1	t
C. du-rietzii		1			1				1		2	1	3	1
C. laricifolia		1	4	1	4	9		1	2	1	6	15	22	6
C. lyalli					3	1					3	1	4	1
C. sessiliflora			2		1						1	2	3	1
C. spectabilis		6	2		8	5		1	1		15	8	23	6
C. viscosa		3	6		8	6			3		11	15	26	8
Coprosma cheesemanii			1									1	1	t
C. pumila					1							1	1	t
Cotula pyrethrifolia						1						1	1	t
Dracophyllum pronum		3	2		3	1		1	2		7	5	12	3
Empetes dieffenbachii		10	10		11	3		1	3		22	16	38	11
Epilobium pedunculare		1	3			2					1	5	6	2
E. perplexum					2						2		2	1
E. rubrum						2						2	2	1
Gaultheria depressa		1	3			1					1	4	5	1
Gentiana corymbifera		6			5			1			12		12	3
Gunnisia caespotosa	1									1			1	t
Plantago novae-zealandiae						1						1	1	t
Pratia angulata					1						1		1	t
Ranunculus ensyii		1									1		1	t
Raoulia grandiflora		1				1			1		1	2	3	1
Schizeilema roughii		1			1						2		2	1
Senecio lagopus		2	2		1	1			1		3	4	7	2
Viola cunninghamii			2						1			3	3	1
Wahlenbergia albomarginata			1		1				1		1	1	2	1
Dicot. flower -unidentified		6	2		4	2			1		10	5	15	4
- A. aromatica		1			1	6		1			9	3	12	3
MOSS & FERN														
Lycopodes australianum		1									1		1	t
L. fastigatum		1									1		1	t
Polytrichum juniperinum		3	2		1	2					4	4	8	2
TOTAL INGESTION	1	65	59	2	99	78		11	30	3	175	170	345	
AV. INGESTION/GRASSHOPPER		23	37		27	36					24	31	27	
SEEDY CROPS									3			3	3	
ARTHROPOD INGESTION					1	1					1	1	2	

Appendix B (Contd.) PLOT A2V2

	ADULT Male Pn	ADULT Male Sa	ADULT Female Pn	ADULT Female Sa	TOTAL Species Pn	TOTAL Species Sa	TOTAL Grand	INGESTION FREQUENCY %
NO. GRASSHOPPERS	8	5	9	8	17	13	30	
INGESTION : MONOCOT								
Chionochloa crassiuscula				1		1	1	1
C. oreophyla	3			2	3	2	5	5
Lachnagrostis forsteri				1		1	1	1
Luzula pumila		1	1		1	1	2	2
L. rufa	2		4	1	4	1	5	5
Poa colensoi		2	5	2	5	4	9	9
P. mackayi				1		1	1	1
Rostkovia gracilis	1		1		2		2	2
Uncinia caespotosa	1	2			1	2	3	3
DICOT								
Aciphylla monroi				1		1	1	1
Anisotome aromatica	1	4	7	6	8	10	18	18
Celmisia dubia				1		1	1	1
C. laricifolia	1	1	1	1	2	2	4	4
C. sessiliflora	1	1	1	1	2	2	4	4
C. spectabilis				1		1	1	1
C. viscosa			3	3	3	3	6	6
Coprosma cheesemanii	1		2		2		3	3
C. pumila	2	1	2	4	1		5	5
Drapete dieffenbachii	3	1	1	1	4	2	6	6
Epilobium rubrum		1				1	1	1
Gaultheria depressa	1		1		2		2	2
Gentiana corymbifera	2		1		3		3	3
Plantago novae-zealandiae	2	1			2	1	3	3
Pratia angulata				2		2	2	2
Ourisia caespitosa			1		1		1	1
O. sessiliflora			1		1		1	1
Senecio scorzoneroides	1				1		1	1
Dicot. flowerparts - unident.	3	1	1	2	4	3	7	7
MOSS & FERN								
Polytrichum juniperinum			1	1	1	1	2	2
TOTAL INGESTION	25	16	32	32	57	43	101	
AV. INGESTION/GRASSHOPPER					34	33	34	
ARTHROPOD INGESTION			1	1	1	1	2	

Appendix B (Contd.) PLOT A23

	ADULT Male			ADULT Female			JUVENILE			TOTAL Species			Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	22	1	1	21	8	16	15	1	1	58	10	18	86	
INGESTION : MONOCOT.														
Astelia nervosa				2						2			2	1
Chionochloa pallens							1			1			1	t
Luzula pumila	3									3			3	1
L. rufa	1			2		1				3		1	4	2
Poa colensoi	1			5	2	2	6		1	12	2	3	17	8
Uncinia caespotosa						1						1	1	t
DICOT.														
Aciphylla monroi					3						3		3	1
Anisotome aromatica	1			7	2	3	1		1	9	2	4	15	7
Celmisia du-rietzii						2						2	2	1
C. laricifolia				1	2	5				1	2	5	8	4
C. sessiliflora				1	2	1				1	2	1	4	2
C. spectabilis		1		2	1	1				2	2	1	5	2
C. viscosa				4	1	2	1			5	1	2	8	4
Coprosma cheesemanii	4						1			5			5	3
C. pumila	3			2		1				5		1	6	3
Dracophyllum pronum	4		1	3	1	4	4	1		11	1	5	19	9
Dracophyllum Dieffenbachii	2		1	1	3		2			5	3	1	9	4
Epilobium pedunculare	1			5	1					6	1		7	3
E. perplexum	2			3	1					5	1		6	3
Gaultheria depressa	3			2		2	1			6		2	8	4
Haastia sinclairii						2						2	2	1
Hebe pinguifolia	2			3			4			9			10	5
Leucogenes grandiceps				1						1			1	t
Ourisia sessiliflora				1	1					1	1		2	1
Ourisia caespotosa	1			1						2			2	1
Pittosporum crassicaule	1									1			1	t
Plantago novae-zealandiae	2									2			2	1
Pygmea pulvinaris	2									2			2	1
Ranunculus ensyii						1						1	1	t
Raoulia grandiflora				1		1				1		1	2	1
Senecio lagopus	1			5	1	3				6	1	3	10	5
Wahlenbergia albomarginata	1		1	4		1				5		2	7	3
Dicot. flowerparts -unident.	8			6	1	2	4		1	18	1	3	22	10
- A. aromatica				2		3				2		3	5	2
MOSS & FERN														
Polytrichum juniperinum				4		1				4		1	5	2
Unidentified moss				1			2			3			3	1
Lichen							1			1			1	t
TOTAL INGESTION	43	1	3	69	22	39	28	1	3	140	23	45	222	
AV. INGESTION/GRASSHOPPER	20			33		24				24	23	25	25	
EMPTY CROPS							1			1			1	
ARTHROPOD INGESTION						2						2	2	

Appendix B (Contd.) PLOT A3

	ADULT Male				ADULT Female				JUVENILE			TOTAL Species				Grand	INGESTION FREQUENCY
	Sv	Bn	Pn	Sa	Sv	Bn	Pn	Sa	Bn	Pn	Sa	Sv	Bn	Pn	Sa		%
NO. GRASSHOPPERS	6	18	26	10	11	22	33	7	7	3	9	17	47	63	26	153	
INGESTION : MONOCOT.																	
Astelia nervosa						1	1						1	1		2	1
Chionochloa crassiuscula		1	1										1	1		2	1
C. oreophylla		3	2				4		1		1		4	6	1	11	3
Luzula pumila		1				1			1				3			3	1
L. rufa		1		1	1	1	1	1	1	1	1	1	3	2	3	9	2
Notodanthonia settifolia				1							2				3	3	1
Poa colensoi	3	6	1	2	1	5	4	2	2		4	4	13	5	8	30	8
P. mackayi				5			1								6	6	2
Rostkovia gracilis	1											1				1	t
Uncinia caespotosa			1	1		2	2						2	3	1	6	2
Monocot. flowerparts		1		1	1	3						1	4		1	6	2
DICOT.																	
Aciphylla monroi	1	1	1	1	3	1	13	1				4	2	14	2	22	6
Anisotome aromatica		2	1	1		4	4	1	1	1			7	5	3	15	4
Brachyscome sinclairii			1				1				1			1	2	3	1
Cardamine hyllobata							3							3		3	1
Celmisia laricifolia		1	1	1		3	1						4	2	1	7	2
C. lyallii			3		1	1	4				1	1	1	7	1	10	3
C. spectabilis			1				2							3		3	1
C. viscosa	1	1	5	4	4	11	9	1			2	5	12	14	7	38	10
Colobanthus acetabulum					1						1					1	t
Coprosma cheesemanii		1	4				3						1	7		8	2
C. pumila		2											2			2	1
Cotula pyrethrifolia	1	1			1							2	1			3	1
Dracophyllum pronum	1	2	1			2	1		1			1	5	2		8	2
Drapetes deiffenbachii		6	1			2	2		1				9	3		12	3
Epilobium crassum					1							1				1	t
E. pedunculare		2	3		1								3	3		6	2
E. perplexum		2		1					2				4		1	5	1
E. rubrum				1											1	1	t
Gaultheria depressa	3	4	4	1		1						3	5	4	1	13	3
Gentiana corymbifera			6	1			5			1	1			12	2	14	4
Haastia sinclairii	1				6				1			7	1			8	2
Hebe cheesemanii					1							1				1	t
H. lycopodioides							1							1		1	t
H. pinguifolia	1	1				1	1					1	2	1		4	1
Leucogenes grandiceps					2	1						2	1			3	1
Ourisa sessiliflora		2											2			2	1
Pratia angulata		1	1			2	1						3	2		5	1
Raoulia grandiflora	1		3		1		2	1			2	2		5	3	10	3
Senecio lagopus	1	1					1	1			1	1	1	1	2	5	1
Viola cunninghamii		4	4	1		3	4						7	8	1	16	4
Wahlenbergia albomarginata		3				2					1		5		1	6	2
Dicot. flowerparts - unident.	3	4	5	3	5	5	4		1			8	10	9	3	30	8
- A. aromatica		1		2	2	5	7	1	2			2	8	7	3	20	5
Unidentified dicot. leaves		1											1			1	t
MOSS & FERN																	
Polytrichum juniperum		4	4	1	1	1	3		1		2	1	6	7	3	17	4
Unidentified moss	1	1						1	1			1	2		1	4	1
Lichen	3		2		1							4		2		6	2
TOTAL INGESTION	18	61	55	29	33	61	84	10	16	3	20	55	137	141	61	393	
AV. INGESTION/GRASSHOPPER		33	21	29	30	28	26					32	29	22	24	26	
EMPTY CROPS								1	1	2	2		1	2	3		
ARTHROPOD INGESTION																	
Diptera							1				1			1	1	2	
Unidentified	1					2	1		1							4	

Appendix B (Contd.) PLOT A3R

	ADULT Male Sv	ADULT Male Bn	ADULT Female Sv	ADULT Female Bn	JUVENILE Sv	JUVENILE Bn	TOTAL Species Sv	TOTAL Species Bn	TOTAL Grand	INGESTION FREQUENCY %
NO. GRASSHOPPERS	18	14	11	7	2	1	31	22	51	
INGESTION : MONOCOT.										
Chionochloa crassinscula				1				1	1	1
Koelaria novae-zealandiae	1						1		1	1
Luzula pumila	1			1			1	1	2	1
L. rufa	4	2	1				4	3	7	5
Notodanthonia settifolia	3	8	1	4	1		5	12	17	12
Poa colensoi	3	3	5	2			8	5	13	9
P. sclerophylla	2	2	2	1	1	1	5	4	9	6
Monocot. flowerparts	1	1		1	1		2	2	4	3
DICOT.										
Aciphylla monroi			1				1		1	1
Anisotome aromatica			1				1		1	1
Celmisia du-reitzii	1						1		1	1
Cotula pyrethrifolia	4	1					4	1	5	3
Dracophyllum pronum	3	3	1	2			4	5	9	6
Hebe cheesemanii	8	8	5	2	1		14	10	24	16
H. pinguifolia	5		1			1	6	1	7	5
Leucogenes grandiceps		1	2	1			2	2	4	3
Pratia angulata		1						1	1	1
Pygmea pulvinaris	2		1				3		3	2
Raoulia bryoides	2		4	1			6	1	7	5
R. grandiflora	4	2	1				5	2	7	5
Senecio lagopus	1		2				3		3	2
Wahlenbergia albomarginata		3		3		1		7	7	5
Dicot. flowerparts Unident.	3		1				4		4	3
-A. aromatica	1						1		1	1
MOSS & FERN										
Polytrichum juniperinum	2	2					2	2	4	3
Unidentified moss		2	1				1	2	3	2
Lichen	1						1		1	1
TOTAL INGESTION	52	42	30	19	4	3	86	62	146	
AV. INGESTION/GRASSHOPPER	29	30	27	27			28	28	29	
ARTHROPOD INGESTION		3						3	3	

Appendix B (Contd.) PLOT A4V

	ADULT Male Pn	ADULT Male Sa	ADULT Female Pn	ADULT Female Sa	JUVENILE Pn	JUVENILE Sa	TOTAL Species Pn	TOTAL Species Sa	TOTAL Grand	INGESTION FREQUENCY %
NO. GRASSHOPPERS	27	20	27	24	6	3	60	47	107	
INGESTION : MONOCOT.										
Chionochloa crassiuscula	7		7	4			14	4	18	9
C. pallens					1		1		1	t
Lachnagrostis forsteri		5		5				10	10	4
Luzula rufa		1						1	1	t
Poa colensoi		2	4	5	2	1	5	8	13	6
P. mackayi	1			1	2	1	3	2	5	2
Uncinia caespotosa	1	1	1			1	2	2	4	2
Unidentified Grass			1				1		1	t
Monocot flowerparts	1						1		1	t
DICOT.										
Aciphylla monroi	4	2	8	5			12	7	19	9
Anisotome aromatica	1		1				2		2	1
Cardamine bilobata	2		1				3		3	1
Celmisia lyallii	7	1	12	6	2		21	7	28	13
C. viscosa	1	7	4	10	1		6	17	23	11
Epilobium rubrum		2						2	2	1
Gentiana corymbifera			2				2		2	1
Pratia angulata	3	3	3	8	1	1	7	11	18	9
Raoulia grandiflora	1	2	1				2	2	4	2
Dicot. flowerparts -unident	1	4	3	5			4	9	13	6
-A.aromatica	6	5	3	8			9	13	22	11
MOSS & FERN										
Polytrichum juniperinum	6	5	1	3			7	8	15	7
Unidentified moss				2				2	2	1
TOTAL INGESTION	42	41	52	62	9	4	102	106	208	
AV. INGESTION/GRASSHOPPER	1·6	2·1	1·9	2·6			1·7	2·3	1·9	
EMPTY CROPS	1	2		1			1	3	4	
ARTHROPOD INGESTION	1		1	2			2	2	4	

Appendix B (Contd.) PLOT A40

	ADULT Male			ADULT Female			JUVENILE			TOTAL Species			Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	11	7	5	2	5	9	1	1	2	14	13	16	43	
INGESTION : MONOCOT.														
Chlonochloa crassiuscula	2	1		1	1	1			1	3	2	2	7	7
C. pallens		1					1			1	1		2	2
Eachnagrostis forsteri						4						4	4	4
Luzula rufa						2						2	2	2
Poa colensoi	1	2	1		3	1			1	1	5	3	9	9
Monocot. flowerparts		1			2	1					3	1	4	4
Unidentified Monocot	1									1			1	1
Aciphylla monroi		1	1		2	2					3	3	6	6
Anisotome aromatica	2		1			1				2		2	4	4
Cardamine debilis	1				1					1	1		2	2
Celmisia lyallii		2			2	1					4	1	5	5
C. viscosa	1	1	2	1	1	3			1	2	2	6	10	10
Epilobium rubrum	1									1			1	1
Gentiana corymbifera		1									1		1	1
Pratia angulata			3			2						5	5	5
Raoulia grandiflora	2	1				1				2	1	1	4	4
Wahlenbergia albomarginata			1			2		1	1		1	4	5	5
Dicot. flowerparts - Unident.	2	4				1	1			3	4	1	8	8
-A. aromatica	6	1	1	2	4	3				8	5	4	17	17
MOSS & FERN														
Polytrichum juniperinum	1			1		3				2		3	5	5
TOTAL INGESTION	20	16	10	5	16	28	2	1	4	27	33	42	102	
AV. INGESTION/GRASSHOPPER	1.8					3.1				1.9	2.5	2.6	2.4	
ARTHROPOD INGESTION				2		2	1			3		2		

Appendix B (Contd.) PLOT A50

	ADULT Male			ADULT Female			JUVENILE			TOTAL Species			Grand	INGESTION FREQUENCY %
	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa	Bn	Pn	Sa		
NO. GRASSHOPPERS	20	19	21	18	33	19	7	4	13	45	56	53	154	
INGESTION : MONOCOT.														
Chionochloa crassiuscula				1	2	1				1	2	1	4	2
C. pallens	1	2		1					1	2	2	1	5	2
Deyuxia avenoides					1						1		1	t
Lachnagrostis forsteri				2	2	3		1	1	2	3	4	9	3
Luzula rufa	2		3		5	3		1		2	6	6	14	4
Notodanthonia setifolia	3	2		5	7	1		1	6	8	10	7	25	8
Poa colensoi	2	3	9	5	12	3	3		3	10	15	15	40	12
P. sclerophylla	1									1			1	t
Rostkovia gracilis			1						1			1	1	t
Uncinia caespotosa	2				3	1			2	2	3	3	8	3
Monocot flowerparts	2			2	2	1				4	2	1	7	2
Unidentified Monocot. leaves					1						1		1	1
DICOT.														
Acinhylla monroi					3	1					3	1	4	2
Anisotome aromatica		2	2		4	6	1		3	1	6	11	18	6
Celmisia lyallii	1	3	2	5	16	6	1		1	7	19	9	35	11
C. viscosa	2	1	2	4		5			1	6	1	8	15	5
Epilobium perplexum		1			3						4		4	2
E. rubrum			1	1						1		1	2	1
Gentiana corymbifera					3						3		3	1
Pratia angulata	6	2	4	4	6	9	1	1	2	12	19	15	36	11
Raoulia grandiflora		4	3	2	1	2				2	5	5	12	8
Viola cunninghamii			1									1	1	t
Wahlembergia albomarginata			1									1	1	t
Dicot. flowerparts - unident.	1		2		2	2				1	2	4	7	2
- A. aromatica	1	3	4	5	3	5	1		4	1	6	13	20	6
MOSS & FERN														
Polystichum cytostegia	3	2		1						4	2		6	2
Polytrichum juniperinum	2	2	6	5	4	7	1		4	3	6	17	26	8
Unidentified moss	2	2	2							2	2	2	6	2
TOTAL INGESTION	31	29	43	43	80	56	10	4	29	72	112	129	321	
AV. INGESTION/GRASSHOPPER	1·6	1·5	2·1	2·4	2·4	3·0				1·7	2·0	2·4	2·1	
EMPTY CROPS							3	1		3	1		4	
ARTHROPOD INGESTION														
Diptera			1	1		1				1		2	3	
Unidentified	2		2	1		3				4		5	9	

Appendix B (Contd.) PLOT TR

	ADULT Male				ADULT Female			JUVENILE		TOTAL Species				Grand	INGEST FREQUEN %
	Sv	Bn	Pn	Sa	Sv	Bn	Sa	Sv	Pn	Sv	Bn	Pn	Sa		
NO. GRASSHOPPERS	3	12	2	1	8	7	1	1	16	12	35	2	2	51	
INGESTION : MONOCOT															
Agropyrum scabrum									1		1			1	1
Luzula pumila		1			1		1			1	1		1	3	2
L. rufa		1		1	1	2			1	1	4		1	6	4
Notodanthonia settifolia		1	1								1	1		2	1
Poa colensoi		3	1		2	1			4	2	8	1		11	8
P. mackayi						1			1		2			2	1
P. sclerophylla									1		1			1	1
Monocot. flowerparts			1									1		1	1
Unidentified grass									1		1			1	1
DICOT.															
Aciphylla monroi				1	1					1			1	2	1
Anisotome aromatica					1	2			2	1	4			5	4
Celmisia laricifolia									1		1			1	1
C. spectabilis		1			1					1	1			2	1
C. viscosa		2				2					4			4	3
Colobanthus acicularis					1	1			1	1	2			3	2
Coprosma cheesmanii			1									1		1	1
C. pseudocuneata					1					1				1	1
Cotula pyrethrifolia	1				1	1				2	1			3	2
Dracophyllum pronum	1			1	1					2			1	3	2
Epilobium rubrum		2				1					3			3	2
Gaultheria depressa		1	2	1					1		2	2	1	5	4
Gentiana corymbifera						1					1			1	1
Haastia sinclairii					1					1				1	1
Hebe cheesemanii			1			1					1	1		2	1
H. epicradea	1		1							1		1		2	1
H. pinguifolia	1	3			2	2		1	5	4	10			14	10
Leucogenes grandiceps					1					1				1	1
Phyllachne colensoi		1							1		2			2	1
Pygmea pulvinaris									1					1	1
Raoulia bryoides					1	1				1	1			2	1
R. grandiflora				1	2	1				2	1		1	4	3
Schizeilema roughii									1					1	1
Senecio lagopus		1				2					3			3	2
Dicot. flowerparts Unident.	2	6			1	5			6	3	17			20	15
fruit -G. depressa		1									1			1	1
MOSS & FERN															
Polytrichum juniperinum	2				1	1			5	3	6			9	7
Unidentified moss					1				1	1	1			2	1
Lichen	1				2			1	1	4	1			5	4
TOTAL INGESTION	9	25	8	5	24	26	1	2	36	34	87	8	6	135	
AV. INGESTION/GRASSHOPPER	30	21			30					28	25			27	
ARTHROPOD INGESTION		1				1			1		3			3	